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Linking climate, arthropod emergence, and fitness in  
snow buntings (*Plectrophenax nivalis*)

by

Peter J. Marier

A Thesis

Submitted to the Faculty of Graduate Studies  
through the Department of Biological Sciences  
in Partial Fulfillment of the Requirements for  
the Degree of Master of Science  
at the University of Windsor

Windsor, Ontario, Canada

2015

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**Linking climate, arthropod emergence, and fitness in  
snow buntings (*Plectrophenax nivalis*)**

by

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24 July 2015

## **DECLARATION OF CO-AUTHORSHIP**

I hereby declare that this thesis incorporates material that is the result of joint research. Both of my data chapters are co-authored with my supervisor, Dr. Oliver Love, and my collaborators, Ms. Christine Madliger and Mr. Chris Harris. In all chapters, the primary ideas, contributions, experimental designs, data analysis, and interpretation are those of the author. Ms. Christine Madliger, Mr. Chris Harris, and Dr. Oliver Love have provided important guidance and feedback in all phases of this project. Dr. Oliver Love has provided the funding, materials, and equipment required to complete this thesis.

I am aware of the University of Windsor Senate Policy on Authorship and I certify that I have properly acknowledged the contribution of other researchers to my thesis, and have obtained written permission from each of the co-authors to include the above materials in my thesis. I certify that, with the above qualification, this thesis, and the research to which it refers, is the product of my own work completed during my registration as a graduate student at the University of Windsor.

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## ABSTRACT

Arctic ecosystems are facing some of the most severe and variable climatic impacts due to climate change. We examined the impact of this climatic variation on arthropod abundance and phenology, and how these relationships impact reproductive decisions and fitness in an Arctic-breeding passerine, the snow bunting (*Plectrophenax nivalis*) using a seven-year dataset from the low Canadian Arctic. Intra- and inter-annual climate-based models yielded significant variation in predictive capacity of arthropod emergence and abundance, limiting their hind- and fore-casting use. At the population level, snow bunting laying decisions appeared constrained by spring temperatures and laying did not appear timed to match nestling peak energy requirements to maximum arthropod availability. However, individual females that timed laying to match peak demand and arthropod abundance had the highest reproductive success, even in low arthropod abundance years. Results highlight the complexities in predicting direct and indirect impacts of climatic variation on Arctic passerine populations.

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# TABLE OF CONTENTS

DECLARATION OF CO-AUTHORSHIP .....	iii
ABSTRACT .....	iv
ACKNOWLEDGEMENTS .....	v
LIST OF TABLES .....	x
LIST OF FIGURES .....	xi
LIST OF APPENDICES .....	xiii
CHAPTER 1 – GENERAL INTRODUCTION .....	1
TIMING OF LIFE HISTORY EVENTS .....	1
SYNCHRONIZATION OF BREEDING AND FOOD RESOURCES .....	2
CONSEQUENCES OF MISTIMING REPRODUCTION TO FOOD RESOURCES ...	3
CLIMATE CHANGE AS A CAUSE OF MISTIMING .....	4
CLIMATE CHANGE-INDUCED MISMATCH OF BREEDING AND FOOD RESOURCES IN BIRDS .....	5
THE ARCTIC AS AN AREA OF CONCERN FOR CLIMATE CHANGE-INDUCED MISMATCH .....	7
OBJECTIVES .....	8
STUDY SYSTEM .....	8
Snow buntings .....	8
Arctic-dwelling arthropods .....	9
East Bay Island .....	10
REFERENCES .....	11

FIGURES .....	16
CHAPTER 2 – INTER-ANNUAL CLIMATIC VARIATION COMPLICATES THE USE OF PREDICTIVE ARTHROPOD PHENOLOGY AND ABUNDANCE MODELS IN AN ARCTIC HABITAT .....	17
INTRODUCTION.....	17
METHODS .....	19
Arthropod Sampling .....	19
Climate Data .....	20
Statistical Analyses .....	20
RESULTS .....	22
Arthropod Emergence and Climate Patterns .....	22
Relative Fitting of the Intra- and Inter-annual Models .....	22
Phenology and Abundance Model Performance .....	22
DISCUSSION .....	23
Model Predictions of Arthropod Emergence Patterns .....	23
Predicting Arthropod Phenology and Abundance .....	24
Conclusion .....	26
REFERENCES.....	27
TABLES.....	31
FIGURES .....	35
CHAPTER 3 – LINKING ARTHROPOD AVAILABILITY AND FITNESS IN SNOW BUNTINGS ( <i>PLECTROPHENAX NIVALIS</i> ).....	38
INTRODUCTION.....	38
METHODS .....	41
Study Species and Reproductive Monitoring .....	41



Arthropod Sampling and Quantification.....	41
Climatic Data .....	42
Statistical Analyses .....	43
RESULTS .....	46
Inter-annual Variation in Breeding Patterns .....	46
Influence of Early Climatic Conditions on Food Resources and Reproductive Timing.....	46
Inter-annual Arthropod Abundance Patterns .....	46
Relationship Between Food Abundance and Reproductive Success.....	46
Effect of Synchronization of Breeding and Food Availability on Reproductive Success.....	47
DISCUSSION .....	47
Inter-annual Breeding Patterns and the Influence of Early Climatic Conditions on Food Resources and Reproductive Timing.....	47
Inter-annual Arthropod Abundance Patterns .....	48
Relationship Between Food Abundance and Reproductive Success.....	49
Effect of Synchronization of Breeding and Food Availability on Reproductive Success.....	50
Conclusion .....	51
REFERENCES.....	52
TABLES.....	57
FIGURES .....	59
CHAPTER 4 – GENERAL DISCUSSION .....	64
SUMMARY AND IMPLICATIONS OF FINDINGS .....	64
LIMITATIONS IN DATA COLLECTION.....	67
Climate-based Predictive Models .....	67

Improving Arthropod and Snow Bunting Sampling.....	68
Individual Variation.....	68
Climatic Data .....	69
Repeated Breeding Data .....	69
CONCLUSION .....	70
REFERENCES .....	71
APPENDICES.....	73
VITA AUCTORIS .....	75

## LIST OF TABLES

Table 2.1 – Total dry biomass of the different arthropod orders and their respective percentage of the total for each sampled year.....	31
Table 2.2 – Climatic variables taken at East Bay Island between 2007-2013.....	32
Table 2.3 – Parameter estimates for the global model (n= 261) and intra-annual models for 2007 (n= 33), 2008 (n= 45), 2009 (n= 33), 2010 (n= 37), 2011 (n= 41), 2012 (n= 33), and 2013 (n= 39). Significant values are bolded.....	33
Table 3.1 – Inter-annual variation in lay date, clutch size, and number of fledglings for snow buntings ( <i>Plectrophenax nivalis</i> ) breeding at East Bay Island, Nunavut between 2007-2013.....	57
Table 3.2 – Generalized linear model for analysis of effect of difference in actual 9 day offspring provisioning arthropod biomass from maximum seasonal 9 day arthropod biomass on reproductive success across three categories of total abundance.....	58

## LIST OF FIGURES

Figure 1.1 – East Bay Island (Mitivik Island) research site. Mitivik Island lies in East Bay in southeast Southampton Island, Nunavut, Canada (Reproduced from Mallory and Fontaine 2004).....	16
Figure 2.1 – Actual total dry arthropod biomass for 2007-2013 [solid line] and predicted arthropod biomass with their respective adjusted $R^2$ model fit values for intra-annual models [dashed line] and global models [dotted line].....	35
Figure 2.2 – Box plot of average arthropod biomass across 2007-2013. Letters denote which years are significantly different by Steel-Dwass test. Hinges indicate lower (25%) and upper (75%) quartile of data, band represents the median, whiskers indicate the position of the 5% quartile and 95% quartile, and dots represent outliers.....	36
Figure 2.3 – Regression between actual quartile day and amount versus the predicted values from the intra-annual models (black) and global model (grey) with their respective adjusted $R^2$ model fit values.....	37
Figure 3.1 – Box plot of (A) average hatch date ( $F= 29.24$ , $df= 6$ , $p= <000.1$ ), (B) average clutch size ( $\chi^2= 21.33$ , $df=6$ , $p= 0.0016$ ), and (C) average number of fledglings ( $F= 5.07$ , $df= 6$ , $p= 0.0002$ ) across 2007-2013. Letters denote years that are significantly different at $p=0.05$ . Hinges indicate lower (25%) and upper (75%) quartile of data, the band represents the median, and whiskers indicate the position of the 5% quartile and 95% quartile.....	59
Figure 3.2 – Regression of mean temperature in late May (May 15-31) with (A) mean hatch date of snow buntings ( $F= 13.46$ , $df= 6$ , $p= 0.0145$ ) and (B) date of 50% quartile arthropod abundance ( $F= 0.94$ , $df= 6$ , $p= 0.38$ ).....	60

- Figure 3.3 – Box plot of average arthropod biomass during offspring provisioning ( $\chi^2=67.18$ ,  $df=6$ ,  $p<0.0001$ ). Letters denote years that are significantly different at  $p=0.05$ . Hinges indicate lower (25%) and upper (75%) quartile of data, band represents the median, and whiskers indicate the position of the 5% quartile and 95% quartile.....61
- Figure 3.4 – Relationship between the mean number of fledglings and (A) total arthropod biomass (GLM;  $F=0.93$ ,  $df=6$ ,  $p=0.47$ ), (B) mean arthropod biomass during offspring provisioning (GLM;  $F=6.03$ ,  $df=6$ ,  $p=0.062$ ), and (C) arthropod biomass during offspring provisioning (GLMM:  $\chi^2=10.45$ ,  $df=2$ ,  $n=78$ ,  $p=0.0054$ ).....62
- Figure 3.5 – Relationship between the number of fledglings and (A) the difference in arthropod biomass during offspring provisioning from maximum amount of biomass possible during high years (2007-2009; solid line), moderate years (2010-2011; dashed line), and low years (2012-2013; dotted line) (GLM;  $\chi^2=10.40$ ,  $df=3$ ,  $p=0.0155$ ) and (B) the difference in arthropod biomass during offspring provisioning from the amount at the 50% abundance quartile (GLM;  $\chi^2=6.03$ ,  $df=3$ ,  $p=0.11$ ).....63

## LIST OF APPENDICES

Appendix A – Correlation of arthropod availability from 2013 and 2014 between East Bay mainland site and East Bay (Mitivik) Island site (Pearson pairwise correlation= 0.80, n= 49, $p < 0.0001$ ).....	73
Appendix B – Correlation of arthropod abundance from 2009-2013 between arthropod sample trap sites (Camera and Nanook ponds) (Pearson pairwise correlation= 0.28, n=225, $p < 0.0001$ ).....	74

# CHAPTER 1 – GENERAL INTRODUCTION

## TIMING OF LIFE HISTORY EVENTS

Determining the factors that limit populations allows for a greater understanding of ecosystem functioning and more effective conservation management of wildlife populations of interest (Newton 1998). Organisms are regulated by biotic and abiotic factors that include resources, competition, predators, parasites, weather, and human-induced disturbance, and the relative importance of these can vary across environments (Dunson and Travis 1991, Newton 1998, Forsman and Mönkkönen 2003). Additionally, the presence or severity of many of these biotic and abiotic factors changes seasonally, constraining the timing of important life cycle events (Stearns 1992). Indeed, many life history events such as emergence, migration, and hibernation (Walther *et al.* 2002, Gienapp *et al.* 2014) occur in a predictable, cyclical manner because they are timed to periods when conditions are most favourable for successful growth, reproduction, and survival (Stenseth and Mysterud 2002, Visser and Both 2005, Lane *et al.* 2012).

Phenology refers to the timing of the seasonal activities (life history events) of organisms, particularly in relation to variation in environmental factors (e.g., temperature, precipitation) (Fenner 1998, Walther *et al.* 2002, Forrest and Miller-Rushing 2010). For example, the timing of major life history events in plants (e.g., leaf expansion, leaf flushing, leaf fall, flower production, seed dispersion) coincides with a particular time of the year (Fenner 1998, Cleland *et al.* 2007), and these events are dictated by prevailing abiotic conditions such as photoperiod, temperature, or precipitation, as well as biotic factors such as herbivory, pollination, and competition (Fenner 1998, Elzinga *et al.* 2007). As such, plants must optimally time the switch between vegetative and reproductive phases to maximize fitness (Cleland *et al.* 2007). As a result, the phenology of many herbivorous species has evolved to match key environmental conditions (Stenseth and Mysterud 2002, Visser and Both 2005, Gienapp *et al.* 2014) since the period of optimal growth and reproduction of herbivores will typically be determined by the phenology of the plants they prey upon (van Asch and Visser 2007). For example, many leaf-eating insects will time their reproduction to synchronize their offspring's

eclosion (emergence of larvae) with bud bursts on host plants to ensure larva have access to the desirable young leaves. If eclosion occurs too early the larvae cannot enter the bud, too late and the leaf becomes too tough, both circumstances resulting in increased mortality (Van Dongen *et al.* 1997, van Asch and Visser 2007). Overall, phenology is a finely tuned process that has evolved to best match life history events with optimal conditions, and a disruption in this timing could have important impacts the survival and reproduction of organisms and the ecosystems they support (Parmesan 2006, Forrest and Miller-Rushing 2010, Lane *et al.* 2012).

## **SYNCHRONIZATION OF BREEDING AND FOOD RESOURCES**

Resources are one of the most crucial factors limiting organismal fitness as they can directly impact survival and breeding success and nutritional resources are particularly important as they are a limiting factor throughout an individual's entire life-cycle (Martin 1987, Newton 1998, Kunz and Orrell 2004). Overall, life histories have evolved to optimize the timing of key events to take advantage of predictable variation in both the timing and abundance of food supply (Stenseth and Mysterud 2002, Varpe *et al.* 2007). Additionally, food availability is particularly vital to individuals during the breeding season as it is required to successfully complete the many energetically-costly reproductive activities such as territory defense, mate attraction, physiological alteration, offspring development, and offspring provisioning (Daan *et al.* 1988, Bennet and Owens 2002, Kunz and Orrell 2004). Furthermore, variation in this food supply (i.e. its abundance and timing) will be a major determinant of breeding in terms of location, schedule, and success (Arcese and Smith 1988, Burke and Nol 1998, Newton 1998, Eeva *et al.* 2000).

Reproduction in migratory birds provides a well-established example of the importance of multi-trophic level phenological synchrony. A characteristic migratory strategy is to temporarily relocate to areas of high productivity to maximize access to food resources during the breeding period (Both and te Marvelde 2007). These highly productive periods typically occur at the beginning of spring when, during a short period of time, vegetation begins to grow and/or prey species begin to emerge, which are used to feed newly hatched offspring (Visser and Both 2005, Both and te Marvelde 2007). As



these decisions must occur far in advance of reproduction for many avian species, they utilize environmental cues such as photoperiod and temperature to fine-tune their life history events to coincide with optimal periods of resource availability (Gwinner 1996, Coppack and Pulido 2004). It is vital for birds living in seasonal environments to correctly time their reproductive events to coincide with resource availability as a higher abundance of resources during these key periods can allow adults to produce and care for more offspring (Newton 1998, McKinnon *et al.* 2012). However, matching the peak of food demand to the peak of food availability is difficult because birds must make their reproductive decisions far in advance since chick rearing takes place several weeks after the birds have initiated egg production and then laid their eggs (Williams 2012).

## **CONSEQUENCES OF MISTIMING REPRODUCTION TO FOOD RESOURCES**

One way that mistiming can have fitness consequences is through its impact on offspring health and survival (McKinnon *et al.* 2012). If hatching does not correspond to peak food availability then there will be less food available during chick rearing, resulting in less resources and a lower survival and fledging success (Thomas *et al.* 2001, Both *et al.* 2005, McKinnon *et al.* 2012). Studies on the Arctic-nesting Baird's sandpiper (*Calidris bairdii*) and Dutch great tit (*Parus major*) have found that an asynchrony of hatch date with insect food peak results in chicks having a lower growth rate and lower mass (McKinnon *et al.* 2012, Visser *et al.* 2006, respectively). A lack of synchrony with peak food availability can also have negative consequences on the rearing parents. Thomas and colleagues (2001) monitored 2 populations of blue tits (*Parus caeruleus*), one on Corsica (a matched population) and the other in Southern France (a mismatched population) and compared the impact of timing on energetic demand of the parents. When breeding date was matched with peak food availability, Corsican blue tits were expending foraging effort similar to other bird species, but when there was a mismatch between nestling demand and prey abundance, Southern France parents had to forage beyond their sustainable limit, resulting in reduced survival (Thomas *et al.* 2001). Therefore, timing reproduction to match resource availability has important impacts on both offspring and parental fitness (Thomas *et al.* 2001, McKinnon *et al.* 2012).

## CLIMATE CHANGE AS A CAUSE OF MISTIMING

The Earth is currently warming at an unprecedented rate (IPCC 2007) and current rises in greenhouse gases are causing global temperatures to increase with correlated changes in vegetation structure, predation, land use, and parasite abundance (IPCC 2007, Mustin *et al.* 2007). The impacts of climate change can be viewed as cascading since climatic shifts (such as surface temperature, precipitation, ocean levels, and terrestrial and sea ice extent) can cause ecological changes (such as droughts, forest fires, flooding) that can ultimately lead to changes that directly impact species survival and individual fitness (Parmesan 2006, Mustin *et al.* 2007). Importantly, because climatic cues provide organisms with information on when to optimize the initiation of specific life history events to maximize fitness (Lechowicz 2002), climate change has altered the phenology of numerous plant and animal species, leading to cascading changes at levels that range from individuals to communities (Walther *et al.* 2002, Cotton 2003). For example, plant phenological events (initiation of leafing and flowering) have been occurring earlier and leaf colouration and leaf fall have been occurring later, resulting in a longer growing season (Khanduri *et al.* 2008). In response, many organisms dependent on plants have advanced their phenological schedules (Walther *et al.* 2002). While overall trends suggest life history events are being advanced, the rate and degree of change exhibited by a given species will determine if a phenological mismatch will occur (Visser and Both 2006).

To determine whether species will shift their phenological schedules in the future, predictive modeling is conducted, which correlates species distributions with climatic indices (Mustin *et al.* 2007, La Sorte and Jetz 2012, Fernandes *et al.* 2013, Warszawski *et al.* 2013). For example, using a predicted climate change scenario from the International Panel on Climate Change (IPCC), the future phenology for both caterpillar and the passerines that depend on them for food has been modeled, predicting that each will advance their phenologies at the same rate and continue to be mistimed unless microevolution occurs (i.e., selection for earlier laying) (Visser *et al.* 2006). Climate change therefore has the strong potential to disrupt life cycles by altering the cues to which life history decisions are predicated; therefore, organisms must be able to adapt to this change or face negative consequences (Walther *et al.* 2002, Parmesan 2006)

## CLIMATE CHANGE-INDUCED MISMATCH OF BREEDING AND FOOD RESOURCES IN BIRDS

The primary reason for the occurrence of phenological mismatches between birds and their prey occurs because the breeding schedules in most bird species are driven by changes in photoperiod (or day length; Dawson *et al.* 2001), whereas the phenological schedules of their prey are largely driven by variation in temperature (Visser *et al.* 2006, Williams *et al.* 2015). Mismatches between reproductive events and resource availability brought on by climate change have been studied in a number of temperate bird species (Visser *et al.* 1998, Cresswell and McCleery 2003, Visser *et al.* 2006). Great tits are a non-migratory insectivorous passerine species that rely on a brief pronounced peak of caterpillar abundance for their young during the breeding season. Climate change has caused caterpillar emergence to advance (in some cases by over a week), creating a need for birds to shift their breeding schedule accordingly (Visser *et al.* 2004, Visser *et al.* 2006). However, a study on a Dutch population of great tits demonstrated that mean lay date (i.e., date of the first egg laid) did not advance despite increases in mean daily spring temperatures, ultimately creating a subsequent mismatch of food availability and offspring demand (Visser *et al.* 2004). In contrast, a study on a UK population of great tits found that lay dates as well as clutch size (and therefore incubation period) was altered based on local temperature to best match caterpillar emergence and as a result, a greater proportion of nests were able to fledge all of their chicks and had more fledglings on average (Cresswell and McCleery 2003). These contrasting results indicate that different populations of the same species may have differential capabilities to adjust breeding phenology in response to climate change.

Climate change poses even greater challenges for long-distance migratory bird species, as in addition to synchronizing their lay date with food availability, they must first time their migration to a disparate site (Visser *et al.* 2004). As such, migratory species facing photoperiodic constraints on the breeding grounds can also face a potential for mismatch when wintering and breeding conditions differ. As with breeding schedules, photoperiodic cues are the major cue for many migrating bird species since the changing length of day provides an indication of when to initiate spring migration towards

breeding grounds (Gwinner 1996) as well as when to time reproduction once they have arrived (Williams 2012). Because day length is unaltered by changes in climate, dependence on this cue could become maladaptive, as changes in daylength cannot convey climate-induced changes on the breeding grounds (Coppack and Pulido 2004). Instead, birds must attempt to fine-tune the timing of their breeding activities based on secondary environmental cues such as temperature. However, there is no guarantee that these climatic conditions are changing similarly on the breeding grounds, which could lead to a mismatch (Coppack and Pulido 2004). Discrepancies in climatic conditions and cues between wintering and breeding grounds have been studied in pied flycatchers (*Ficedula hypoleuca*), a long-distance insectivorous migratory bird that winters in North Africa and breeds throughout Europe and western Asia (Lundberg and Alatalo 1992, Both and Visser 2001). They time their long migration to their European breeding grounds to coincide with increases in arthropods to feed their young (Lundberg and Alatalo 1992, Both and Visser 2001). A 20-year study revealed that these birds have advanced their lay date by approximately 1 week, but not sufficiently enough to keep pace with the changing emergence of their food supply, which has advanced nearly 2 weeks (Both and Visser 2001). This insufficient response is proposed to be constrained by migration schedule, which did not change during the study period as it is triggered by day-length variation, which has remained constant (Gwinner 1996, Both and Visser 2001). These results demonstrate a principal issue for long-distance migrants: the environmental conditions and changes in wintering grounds and along migration routes are dissimilar from those at breeding grounds, causing an uncoupling of synchrony (Both and Visser 2001). While long-distance migrants seem to be constrained in their arrival, short-distance migrants, and those that utilize stop-over and staging sites may be more responsive to climate warming as many studies have demonstrated earlier arrival dates for these species (Walther *et al.* 2002, Dunn 2004, Visser and Both 2005). This is likely due to the higher similarity of climatic cues in sites closer to the breeding area (Both and Visser 2001). Lastly, when examining 100 European bird species since 1960 to determine whether there was a link between phenological responses and population trends, Møller *et al.* (2008) found that between 1990-2000, species that did not advance their spring migration were declining whereas those that advanced their migration showed a stable or

increasing population. Taken together, these results demonstrate that further climate change could threaten bird populations and highlights the importance of response in the face of a changing and variable climate.

## **THE ARCTIC AS AN AREA OF CONCERN FOR CLIMATE CHANGE-INDUCED MISMATCH**

Although avian responses to climate change have been well-studied in a number of temperate avian species (e.g., great tit, blue tit, pied flycatcher), comparatively little work has been conducted in Arctic systems. However, the ecological impacts of climate change are far more pronounced in polar regions where dramatic increases in mean and intra-annual variation in climatic indices (temperature, ice/snow cover, precipitation) are resulting in downstream effects on ecosystems, such as changes in wildlife phenology and distribution (Parmesan 2006, Post *et al.* 2009). Unfortunately, very little is known regarding the mechanisms linking climatic variation and fitness in Arctic-breeding insectivorous birds. Nevertheless, these species are likely at greatest risk of phenological mismatches due to the short growing season which limits the phenological flexibility of individuals and constrains them to a single reproductive event per year (Martin and Wiebe 2004, Pearce-Higgins *et al.* 2005, Both *et al.* 2009). Moreover, these birds are likely highly constrained by environmental conditions as to when they can initiate reproduction (as delaying is often not an option), further compromising their ability to match the ephemeral availability of their food supply on the breeding grounds (Eeva *et al.* 2000). Indeed, evidence is mounting that Arctic populations of avian species are declining precipitously. For example, in a survey of 35 Canadian shorebird species (the majority of which breed in Arctic ecosystems), 28 (80%) exhibited a statistically significant decline while only one demonstrated an increase (Donaldson *et al.* 2000). Similarly, a study of insectivorous migrant passerine species in the Netherlands reported a large decline over a 20-year period in long-distant migrants residing in highly seasonal forested environments (as in the Arctic) but not in those in less seasonal marshes (Both *et al.* 2009). It has been shown previously that Arctic birds face similar fitness consequences in the event of a phenological mismatch as their temperate counterparts and

as a result, it is critical to understand how species breeding in these extreme environments are responding to climate change (McKinnon *et al.* 2012).

## **OBJECTIVES**

Our overall objective was to investigate the links between climate, arthropods, and Arctic-breeding passerines by examining 1) how variation in climate impacts the abundance and timing of emergence of Arctic arthropods; and 2) how arthropod timing and abundance affect an Arctic songbird's reproductive success and the importance of synchronizing breeding to this ephemeral food resource. To investigate the capacity of climatic variables to influence and predict Arctic arthropod emergence patterns, we developed predictive models using a seven-year arthropod dataset collected in the low Canadian Arctic (Chapter 2). These models were then compared and assessed on their ability to accurately predict arthropod abundance and phenology. Next, to determine the potential impact of phenological and abundance mismatches between an Arctic-breeding bird species and their prey, we examined the effect of arthropod availability during the breeding season on the reproductive success of a snow bunting population (Chapter 3). Lastly, we provide a discussion of the implications and limitations of our study as well as suggestions for how future work in this field can further examine the vulnerability of Arctic-breeding avian systems to climate-induced variability (Chapter 4).

## **STUDY SYSTEM**

### **Snow buntings**

Snow buntings (*Plectrophenax nivalis*) are a circumpolar Arctic-breeding passerine. In North America, they winter in southern Canada and the northern United States (Macdonald *et al.* 2012, 2015). They are the earliest-arriving spring avian migrant to the Arctic, the timing of which is linked with snowmelt given that individuals feed on insects along the margins of snow free areas (Montgomerie and Lyon 2011). Males arrive on breeding grounds several weeks prior to females to establish territories and compete for high-quality breeding sites (Tinbergen 1939, Salomonsen 1950, Meltofte 1983, Macdonald *et al.* 2012). Females build nests and produce a single clutch per season

containing 5-7 eggs (Montgomerie and Lyon 2011). Snow buntings are income-breeders, i.e. the resources used for egg formation originate entirely from biomass gained on breeding grounds (Moltofte *et al.* 2007). At hatching, both parents feed nestlings arthropods, almost exclusively from the order *Diptera* (flies) (Parmelee 1968). Recent data from the Christmas Bird Count indicates that North American populations are in serious decline (approximately 64% decline in the past 40 years) (Butcher and Niven 2007). Although climate change has been proposed as an obvious cause (Butcher and Niven 2007), no studies have examined the mechanisms by which declines may be driven, or at what life-history stages these possible effects may be occurring.

### **Arctic-dwelling arthropods**

There are more species of insects that dwell in the Arctic than any other animal and they are known to form some of the most important prey bases in these systems (Danks 2004, Legagneux *et al.* 2012). As arthropods are poikilothermic (where internal temperature varies with the ambient temperature of their surroundings), they are expected to be among the most affected by climate change since their physiology, timing of emergence, and abundance are all intimately linked to temperature (Høye and Forchhammer 2008, Tulp and Schekkerman 2008, Williams *et al.* 2015). Due to the subzero temperatures prevalent throughout most of the year in the Arctic, many arthropod species residing in this area (for example: spiders, *Diptera*, and *Lepidoptera*) have a lengthy winter dormancy and multi-annual life cycles (Høye and Forchhammer 2008). Many deposit their eggs or larvae during the summer where they will overwinter as eggs, larvae, pupae, or inactive adults (Tulp and Schekkerman 2008). Adults emerge when prevailing conditions are optimal (such as a peak in food resources or availability of mates and egg-laying habitats) and devote their time almost exclusively to reproduction, causing the characteristic short burst of arthropod abundance (Høye and Forchhammer 2008, Tulp and Schekkerman 2008). As this contracted period of adult emergence is likely governed primarily by the rise in temperature and subsequent snowmelt, climate change will likely cause this period to become more variable across years and cause a mismatch with the species that prey upon them (Høye and Forchhammer 2008, Tulp and Schekkerman 2008, Bolduc *et al.* 2013).

## **East Bay Island**

Snow bunting and arthropod data collection was conducted on East Bay (Mitivik) Island (64°02'N, 81°47'W), Nunavut, Canada (Figure 1.1). East Bay Island is ideal for focal research questions for a number of reasons: 1) the abundance of loose granite rock provides ample ideal nesting sites for snow buntings, allowing for a high breeding density; 2) the presence of multiple ponds from which arthropods emerge provides an easily-accessible source of food for buntings and an accurate location for sampling and determining arthropod availability; 3) a lack of mammalian predators removes confounding sources when determining reproductive success; and 4) the island's small size allows for precise monitoring of all individuals.



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## FIGURES

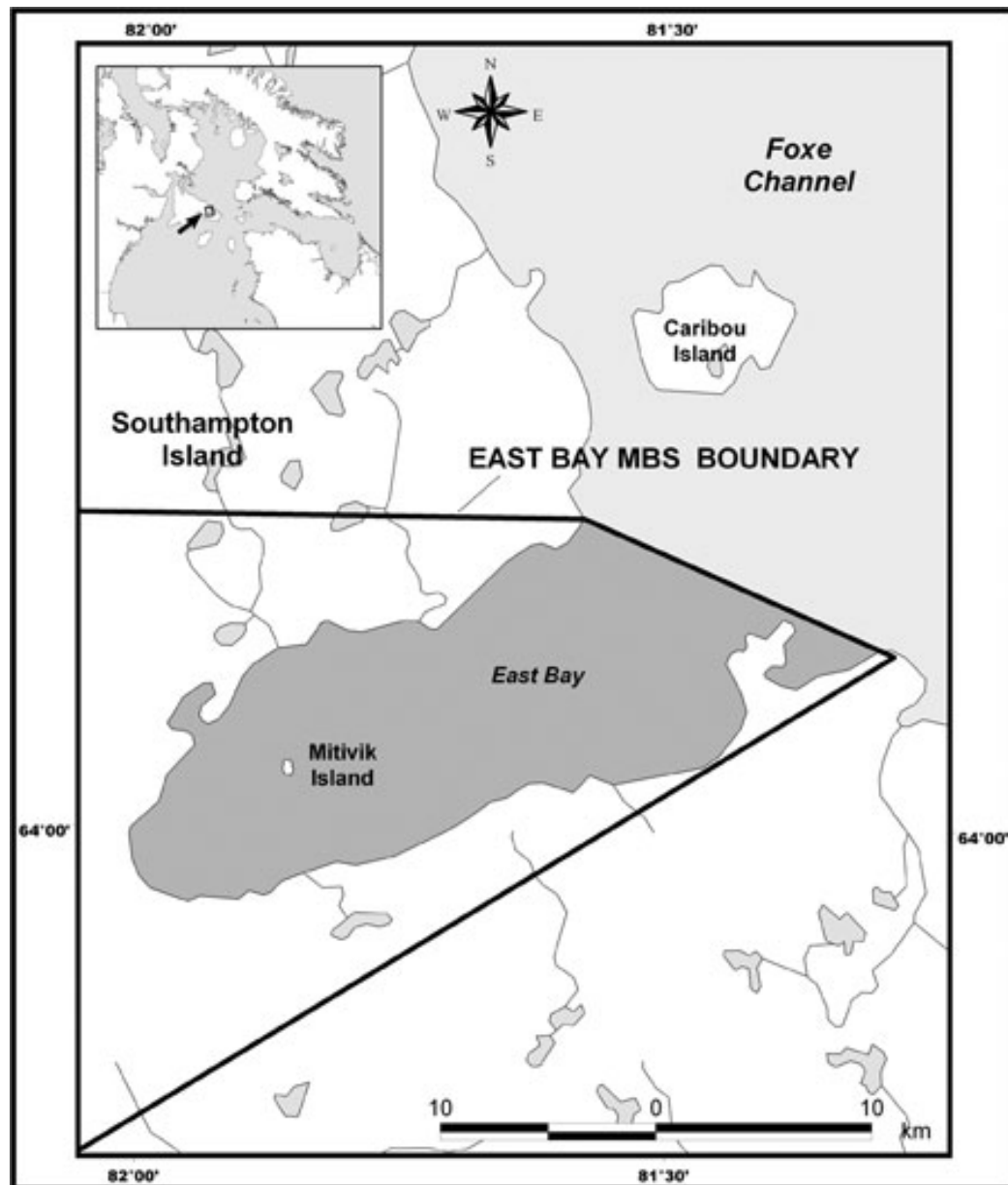


Figure 1.1 – East Bay Island (Mitivik Island) research site. Mitivik Island lies in East Bay in southeast Southampton Island, Nunavut, Canada (Reproduced from Mallory and Fontaine 2004.)

# **CHAPTER 2 – INTER-ANNUAL CLIMATIC VARIATION COMPLICATES THE USE OF PREDICTIVE ARTHROPOD PHENOLOGY AND ABUNDANCE MODELS IN AN ARCTIC HABITAT**

## **INTRODUCTION**

Climate change and its associated ecological impacts are being most dramatically experienced in the polar regions of the planet (IPCC 2007). Arctic ecosystems are facing some of the most intense and variable climatic impacts and these trends are only predicted to increase in the future (Callaghan *et al.* 2005, IPCC 2007). This disproportionate degree of rapid climatic change is already causing numerous downstream effects on Arctic ecosystems, including impacts on wildlife phenology, distribution, and productivity (Berteaux *et al.* 2006, Post *et al.* 2009, McKinnon *et al.* 2013, Legagneux *et al.* 2014). Poikilotherms (where organismal temperature variation is a consequence of variation in the ambient environmental temperature), such as arthropods, are expected to be among the most affected by climate change, since their physiology, timing of emergence, and abundance are all intimately linked to temperature (Høye and Forchhammer 2008, Tulp and Schekkerman 2008, Bolduc *et al.* 2013, Williams *et al.* 2015). Although the level of Arctic ecosystem linkages is complex (Hodkinson and Coulson 2004, Gauthier *et al.* 2012, Legagneux *et al.* 2012), arthropods are known to form some of the most important prey bases in these systems (Legagneux *et al.* 2012, McKinnon *et al.* 2013). For example, the successful reproduction and offspring survival/recruitment of numerous Arctic-breeding insectivorous birds, including songbirds, shorebirds, and waterfowl, have been linked to the brief, but highly productive period of arthropod abundance during the short Arctic summer (Pearce-Higgins *et al.* 2005, Falconer *et al.* 2008, McKinnon *et al.* 2012, 2013).

There is substantial evidence that numerous types of temperate environments have been experiencing earlier emergence of arthropods in response to warming local temperatures, ultimately resulting in a temporal mismatch with bird populations that

depend on them during their reproductive period (Both and Visser 2001, Visser *et al.* 2004, Visser *et al.* 2006). Temperate areas are often characterized by a defined peak of arthropod biomass (Stenseth and Mysterud 2002, Visser *et al.* 2004) and as such, predicted mean temperatures have been used to forecast future peak periods (Visser *et al.* 2006). Unfortunately, our understanding of the impacts of changing climate on Arctic arthropod phenology and abundance is currently limited. A stronger understanding of whether climatic variation predicts arthropod phenology and abundance will help to determine the mechanisms underlying climate-arthropod-vertebrate phenology relationships (e.g., Visser *et al.* 2004, Both *et al.* 2005), allowing for a more effective means of monitoring Arctic ecosystems by more accurately forecasting future conservation and biodiversity scenarios (Hannah *et al.* 2002, Huntley *et al.* 2004, Mustin *et al.* 2007, Andrew *et al.* 2013).

Various predictive modeling approaches have been developed to examine the link between climatic variability and arthropod emergence, including species distribution models (or niche models), which correlate current species distributions with climate variables to generate predicted species' distributions (Mustin *et al.* 2007). Importantly, these models can theoretically be used to hindcast expected distributions in years where species data are not available (Tulp and Shekherman 2008), to forecast future biodiversity based on climate change models (La Sorte and Jetz 2012, Warszawski *et al.* 2013), or as an overall tool to assess impacts of climate on ecosystems and their respective trophic interactions (Bolduc *et al.* 2013, Fernandes *et al.* 2013). However, since the predictive capacity of these models is expected to vary depending on the climate variables used and the number of years included (Tulp and Shekherman 2008), researchers need to test: 1) how and why these models succeed or fail to predict key arthropod metrics within and across study years, and 2) the relative success of these models at predicting two important, but very different, arthropod emergence metrics – phenology and abundance. The latter investigation is important since the relative roles of arthropod phenology and abundance in impacting the reproductive success of Arctic-breeding vertebrate species may be quite different to those seen in temperate systems.



Here, we use a 7-year dataset to examine the capacity of climatic variables to predict arthropod emergence patterns both within and across years in the low Canadian Arctic. We further evaluate the ability of intra-annual and multi-year models to predict insect phenology and abundance. We 1) modeled emergence patterns to determine if intra-annual and multi-year models could be used to simulate actual arthropod emergence patterns; and 2) extracted specified phenology and abundance metrics to evaluate the relative predictive effectiveness of climate models. Given the importance of temperature to arthropods, as well as the harsh climate and constrained growing season in the Canadian Arctic, we predicted that while intra-annual models may differ, a multi-year global model using climatic variables would be sufficient to predict the general trend of arthropod abundance and phenology.

## **METHODS**

### **Arthropod Sampling**

Sampling was conducted in the Canadian low Arctic in Nunavut within the East Bay Migratory Bird Sanctuary, Southampton Island, at two sites separated by 5km (East Bay mainland site – 63°59'N, 81°40'W – 2007 and 2008; East Bay (Mitivik) Island site – 64°02'N, 81°47'W – 2009-2013). These two sites are significantly correlated in arthropod abundance (Appendix A). Arthropod samples were collected using passive modified pitfall traps (as outlined in Bolduc *et al.* 2013). Traps are composed of a plastic tube frame approximately 35 x 35 cm with a fine mosquito mesh placed upright directly over a plastic pitfall trough. The mesh is covered by an inverted plastic cone that funnels flying insects up to a collection bottle. The trap captures ground-dwelling arthropods which fall directly into the pitfall as well as low-flying arthropods which hit the mesh and either fall into the trough or climb to the collection bottle. Capture totals from modified pitfall traps incorporate both density and activity levels of surface-dwelling arthropods, and can therefore be used as a reliable proxy for arthropod availability at sampling sites (Southwood and Henderson 2000). Sampling periods were chosen to best match migrating passerine and shorebird arrival/breeding dates from early June to late July in each year. Collection at the mainland site was conducted in low wetland tundra (2007 – 5

traps, 2008 – 3 traps) and at the island site in low wetland tundra adjacent to 2 small ponds, Camera pond and Nanook pond (2009-2013 – 4-8 traps). These 2 pond sampling locations are significantly correlated in arthropod abundance (Appendix B). Traps were visited every two days, and samples were collected and stored in ethanol (70%) until quantification and identification in the laboratory. Arthropods were sorted to order, true spiders (*Araneae*) were grouped together, and springtails (*Colembola*) and mites (*Acari*) were excluded due to their negligible contribution to overall biomass. Each order from samples from 2009-2013 were dried in pre-weighed paper envelopes at 50°C for 5 days and weighed using an electronic balance to the nearest 0.01 mg. Dry biomass values for samples from 2007 and 2008 were obtained by converting arthropod counts using length-dry mass equations (Bolduc *et al.* 2013, McKinnon *et al.* 2012). Biomass totals for all arthropods collected were determined and arthropod availability was calculated by dividing total arthropod biomass by the number of traps sampled and by the number of days between changing the collection vessel, and is therefore presented as arthropod availability in mg/trap/day.

## **Climate Data**

Climatic variables were selected based on previously published work that demonstrated the ability of predictive models to use climatic variables to predict current and past Arctic arthropod availability (Tulp and Shekkerman 2008, Bolduc *et al.* 2013). Climatic variables were chosen in the form of mean daily weather data known to influence arthropod phenology and abundance: air temperature in °C, wind speed in km/h, precipitation in mm, and relative percent humidity (Høye and Forchhammer 2008, Tulp and Shekkerman 2008, Bolduc *et al.* 2013). These were obtained from daily recordings gathered from a Davis Vantage Pro automated weather station on East Bay Island.

## **Statistical Analyses**

As daily biomass values were non-normal, a Kruskal-Wallis with a Steel-Dwass post-hoc test was used to investigate differences in average arthropod biomass across

years. To test the capacity of climate variables to predict arthropod emergence patterns, we then created intra-annual generalized linear models with a Poisson distribution (to account for non-normally distributed count data) for the daily biomass of all sampled arthropods through each season. Climatic variables used to populate our models included: mean daily temperature, mean wind speed (to account for variation surrounding arthropod trap success), relative humidity, precipitation, and Julian date. We also included the quadratic form of the climatic variables to account for non-linear patterns of climate on arthropod emergence patterns (Tulp and Shekkerman 2008, Bolduc *et al.* 2013). To determine whether any of our independent variables were significantly inter-correlated we ran a pairwise Pearson correlation and subsequently calculated the Variance Inflation Factors (VIF). Thaw-degree days (a measure of warming after melt) was originally included in the model (as well as its quadratic form), but was ultimately removed due to having a VIF of over 5. To create a model which was more broadly applicable and capable of extrapolating beyond our dataset, we also produced a global predictive model with all years of data combined using a generalized linear mixed model with a Poisson distribution (with year as a random effect) using the same climatic variables as the intra-annual models.

To test the ability of the intra- and inter-annual models to predict the timing of emergence (i.e., phenology) and the abundance of arthropods over this emergence, we calculated quartiles of abundance for each year, i.e. when 25%, 50%, and 75% of the total catch was obtained, as these provide an objective means of quantifying seasonal development of capture numbers (Høye and Forchhammer 2008). As logistical limitations and the need to match timing with avian study species meant that the sampling season did not begin and end on the same date every year, the first and last sampling date used were kept constant for every year to enable inter-annual comparisons. Since arthropod abundance is typically low in the early sampling period, only 4.3% of the total biomass was excluded in standardizing the sampling period. The Julian date and abundance of each quartile (as well as the total biomass for the season) were determined for both the actual sampled amounts and predicted amounts generated from the intra-annual and global models. The relative ability of both the intra-annual and global model

approaches to predict arthropod phenology and abundance was then assessed as a measure of a given model's fit (linear regression – adjusted  $R^2$ ) between the generated model-predicted arthropod phenology/abundance and the actual phenology/abundance. All analyses were performed in JMP 12 (SAS Institute).

## RESULTS

### Arthropod Emergence and Climate Patterns

We detected a large degree of inter-annual variation in the emergence patterns of arthropods collected at East Bay, Nunavut (Figure 2.1) with a five-fold difference in the total amount of arthropods sampled among years and significant differences between years ( $\chi^2 = 73.32$ ,  $df=6$ ,  $p < 0.0001$ , Figure 2.2). With regards to arthropod diversity, *Diptera* (true flies) was consistently the most abundant order, followed by *Coleoptera* (beetles), although the relative abundance of orders varied by year (Table 2.1). In terms of climate, there was considerable inter-annual variation in all of the variables we tested (Table 2.2).

### Relative Fitting of the Intra- and Inter-annual Models

Both intra-annual models and the global model relating climatic variables to arthropod emergence were all highly significant (Table 2.3). Julian date and mean daily temperature (and their quadratic forms) had the highest model inclusion rates; however, no single variable was consistently included across all models (Table 2.3). Additionally, models varied greatly in their capacity to predict actual arthropod emergence patterns (Figure 2.1) and intra-annual models produced better fits than the multi-year model. For example, (adjusted  $R^2$ ) model fits for intra-annual models of arthropod biomass ranged from 0.52 to 0.85, whereas global models fit consistently worse, ranging from 0.18 to 0.56 in the same years (Figure 2.1).

### Phenology and Abundance Model Performance

Intra-annual models were able to predict arthropod phenology: the regressions of the Julian dates that correspond to the quartiles of the actual arthropod data and those

same dates predicted by the intra-annual models were highly significant ( $p < 0.0001$ ), with model fits ranging from 0.96-0.98 (Figure 2.3). However, the global model was generally unable to predict arthropod phenology, as predicted Julian dates from the global model were only significantly related to actual dates for the 25% quartile ( $F = 6.84$ ,  $p = 0.0474$ , adjusted  $R^2 = 0.49$ ; Figure 2.3).

Similarly, intra-annual models were able to predict arthropod abundance: the regressions between the total accumulated biomass corresponding to the quartiles of the actual arthropod data and the cumulative biomass values generated by the intra-annual models were highly accurate ( $p < 0.0001$ ), all having model fits (adjusted  $R^2 > 0.99$  (Figure 2.3). Again, similar to phenology, the global model was unable to predict arthropod abundance: the regressions of values at the quartiles were all non-significant with poor model fits (Figure 2.3).

## DISCUSSION

### Model Predictions of Arthropod Emergence Patterns

In a seven-year data set from the low Canadian Arctic, patterns of arthropod emergence were extremely variable across years, although relative richness was reasonably stable (i.e., comprised of the same primary orders each year despite variation in their relative proportion to the total biomass). This variability of arthropod emergence patterns is congruent with those of other studies in the Arctic (Høye and Forchhammer 2008, Tulp and Schekkerman 2008, Bolduc *et al.* 2013). At East Bay, the overall abundance appears to be driven primarily by a few key arthropod orders, namely *Diptera*, *Coleoptera*, and in some years *Araneae*. Our models suggest that there is a close link between arthropod emergence patterns and several climatic factors, especially – but not surprisingly – temperature. However, the specific individual climatic factors that are linked to arthropod emergence appear to vary greatly by year, and no single variable was consistently included across all models. Intra-annual models predicted arthropod abundance with an accuracy of 76% or greater in 5 of the 7 years tested. However, while these within-year models are useful for disentangling the short-term impacts of climate

on arthropod population dynamics, they cannot be used in a predictive capacity across years when arthropod counts are unknown. To effectively hind- or forecast arthropod abundance, models must instead be based on an existing and consistent relationship across multiple years as in our global models. Global multi-year models can serve a crucial role in future ecological studies, as they can provide insight on how large-scale changes (such as climate) can impact various taxa at different stages and ultimately aid in our understanding of conservation of threatened species (McMahon *et al.* 2011). The caveat to using these tools is that they first must be tested to ensure that a single model is able to fit different years of known data with equal consistency across years.

Unfortunately, the global model we tested was consistently less accurate at predicting arthropod availability than our intra-annual models (mean adjusted  $R^2$  for global models =  $0.436 \pm 0.203$  vs. mean adjusted  $R^2$  for intra-annual models =  $0.724 \pm 0.135$  for total arthropod biomass). While it may not be surprising that a multi-year model would be less accurate than a within-year model in a highly variable system such as the Arctic, the relatively low predictive capacity of the multi-year model calls into question the usefulness of models utilizing only climatic variables for accurately hind- and forecasting Arctic arthropod phenology and abundance.

## **Predicting Arthropod Phenology and Abundance**

To further investigate the performance of the models, we extracted key predicted measures of phenology and abundance through the arthropod sampling season. Since our Arctic site does not display consistent and identifiable ‘peaks’ of arthropod abundance, values at the quartiles of abundance (i.e. when 25%, 50%, and 75% of the total arthropod catch was obtained) were extracted. The quartile values from the sample data were compared to those of the predictive models to test the relative capacity of these models to accurately predict actual arthropod phenology and timing. Being able to predict these metrics with models is important because it allows us to pinpoint specific time points of interest as well as the overall availability of arthropods during the season in order to uncover potential trends and relationships with threatened taxa or impacts of alterations brought about by climate change. While intra-annual models were able to predict arthropod phenology very accurately (mean fit = 0.968), the global model failed to

significantly predict any quartile values of timing except for early in the season (25% quartile) and even then, with a fit of only 0.493. The intra-annual models were also highly accurate at predicting arthropod abundance throughout the entire season (fit=0.999), while global models were unable to significantly predict abundance at any point. This demonstrates that when insect biomasses are extremely variable across years, global models have difficulty predicting arthropod phenology, more so as the season progresses, and are unreliable at predicting the abundance of arthropods during a season. These difficulties further suggest that factors that govern arthropod phenology and abundance are likely linked and vary considerably across years.

We also detected inconsistency in which climatic variables were significant in the predictive models. Variables, such as Julian date (i.e., progress through the season) and temperature, that have previously been demonstrated to play a key role in arthropod activity (Hodkinson *et al.* 1996, Tulp and Schekkerman 2008), contributed significantly to the models in some years, but not in others. This suggests that different climatic variables are linked to arthropod emergence patterns in different years, and that no single climatic variable is consistently impacting their activity and therefore, their emergence patterns. This ultimately makes it more difficult, and therefore more unlikely, that one overall global model will be capable of predicting arthropod emergence patterns, and therefore phenology, accurately. Although the matching of vertebrate breeding phenology to coincide with arthropod phenology has been shown to be important for successful reproduction and fitness in a number of temperate avian species (Thomas *et al.* 2001, Visser and Both 2005, Visser *et al.* 2006, McKinnon *et al.* 2012, Gienapp *et al.* 2014), it remains to be seen whether it is the phenology or the abundance of arthropods which has a greater impact on the reproductive output of Arctic-breeding birds. It should also be noted that the current models were constructed using only a seven-year data set and we would therefore expect some degree of improvement in their predictive capacity with additional years of data.

## Conclusion

While Arctic food webs may appear relatively simple in overall structure, they are complex in terms of how their components interact with each other and the environment (Gauthier *et al.* 2012, Legagneux *et al.* 2012, 2013). Moreover, although climatic variation has been shown to be a primary regulating factor in arthropod phenology (Bolduc *et al.* 2013, McKinnon *et al.* 2013), our model comparisons suggest models developed from climatic measures alone should be used with caution to hind- or forecast Arctic arthropod availability (both in terms of phenology and abundance), as these climatic factors are variable in their importance across years. Further investigations into the mechanisms underlying temporal and spatial variation in Arctic arthropod phenology and abundance are needed, as they will significantly aid in our understanding of their interaction and role in driving the demography of the larger Arctic ecosystems they support.



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## TABLES

Table 2.1 – Total dry biomass of the different arthropod orders and their respective percentage of the total for each sampled year.

Year	Diptera		Coleoptera		Hymenoptera		Hemiptera		Lepidoptera		Tricoptera		Aranae		Total
	mg/year	%	mg/year	%	mg/year	%	mg/year	%	mg/year	%	mg/year	%	mg/year	%	mg/year
2007	2243.58	70.06	598.05	18.68	17.70	0.55	26.06	0.81	0.00	0.00	9.40	0.29	307.54	9.60	3202.33
2008	1773.90	74.54	193.33	8.12	53.23	2.24	42.77	1.80	63.43	2.67	29.03	1.22	223.60	9.40	2379.30
2009	3201.58	86.71	384.08	10.40	51.93	1.41	49.64	1.34	3.86	0.10	1.24	0.03	0.00	0.00	3692.33
2010	987.00	63.45	377.14	24.24	53.60	3.45	78.17	5.03	0.00	0.00	0.00	0.00	62.74	4.03	1558.65
2011	874.99	54.66	372.44	23.27	120.88	7.55	120.51	7.53	0.00	0.00	2.58	0.16	109.31	6.83	1600.70
2012	384.93	55.84	194.95	28.28	12.43	1.80	19.63	2.85	0.00	0.00	0.00	0.00	77.35	11.22	689.28
2013	520.74	75.14	105.65	15.24	16.83	2.43	11.79	1.70	0.00	0.00	0.00	0.00	38.00	5.48	693.00
2014	882.32	76.38	98.91	8.56	20.43	1.77	21.91	1.90	0.00	0.00	0.00	0.00	132.19	11.44	1155.75

Table 2.2 – Climatic variables taken at East Bay Island between 2007-2013.

Year	Temperature (°C)				Wind Speed (km/h)				Precipitation (mm)				Humidity (%)			
	Min	Max	Mean	SE	Min	Max	Mean	SE	Min	Max	Mean	SE	Min	Max	Mean	SE
2007	0.87	12.64	4.3	0.48	4.72	35.33	14.37	1.49	0	0.17	0.02	0.01	76.4	95.94	90.28	0.87
2008	0.56	11.91	5.44	0.54	1.57	27.23	12.08	0.97	0	0.58	0.02	0.01	77.96	95.02	86.55	0.77
2009	2.22	12.05	6.56	0.45	2.9	19.77	8.73	0.92	0	0.09	0.003	0.003	68.35	93.04	83.75	0.99
2010	1.24	11.89	5.13	0.45	1.8	30.03	10.37	1.07	0	0.01	0.001	4E-04	69.02	94.65	84.94	0.9
2011	1.52	11.5	6.37	0.45	4.14	40.94	12.99	1.37	0	0.3	0.02	0.01	68.38	93.1	83.79	0.83
2012	1.33	10.96	4.35	0.45	3.48	31.95	13.69	1.51	0	0.25	0.03	0.01	94	94	94	0
2013	1.05	13.98	4.73	0.39	3.77	35.54	15.86	1.22	0	0.14	0.01	0.005	24.21	72.69	39.73	1.67

Table 2.3 – Parameter estimates for the global model (n= 261) and intra-annual models for 2007 (n= 33), 2008 (n= 45), 2009 (n= 33), 2010 (n= 37), 2011 (n= 41), 2012 (n= 33), and 2013 (n= 39). Significant values are bolded.

Parameters	Global Model				2007 Model				2008 Model				2009 Model			
	Est.	SE	$\chi^2$	<i>p</i>	Est.	SE	$\chi^2$	<i>p</i>	Est.	SE	$\chi^2$	<i>p</i>	Est.	SE	$\chi^2$	<i>p</i>
Intercept	-113.22	19.81	38.68	<b>&lt;.0001</b>	-158.46	93.40	3.08	0.08	-206.16	58.32	16.34	<b>&lt;.0001</b>	-187.84	58.53	10.82	<b>0.001</b>
Julian Date	1.17	0.21	38.16	<b>&lt;.0001</b>	1.07	0.64	2.98	0.08	2.10	0.36	47.15	<b>&lt;.0001</b>	2.07	0.55	15.32	<b>&lt;.0001</b>
Julian Date <sup>2</sup>	-0.0030	0.0005	36.95	<b>&lt;.0001</b>	-0.0027	0.0017	2.69	0.10	-0.0054	0.0009	46.25	<b>&lt;.0001</b>	-0.0054	0.0014	15.74	<b>&lt;.0001</b>
Temperature	0.29	0.09	11.72	<b>0.0006</b>	-0.01	0.25	0.0029	0.96	-0.03	0.24	0.02	0.90	0.25	0.17	2.18	0.14
Temperature <sup>2</sup>	-0.02	0.0061	7.94	<b>0.0048</b>	0.0068	0.02	0.10	0.75	0.0066	0.02	0.19	0.66	-0.01	0.01	1.33	0.25
Wind Speed	-0.04	0.03	2.21	0.14	0.06	0.07	0.70	0.40	-0.06	0.05	1.30	0.25	0.03	0.08	0.10	0.75
Wind Speed <sup>2</sup>	-0.0005	0.0009	0.37	0.54	-0.0041	0.0024	3.39	0.07	0.0006	0.0022	0.08	0.78	-0.0010	0.0045	0.05	0.83
Precipitation	5.70	2.36	5.31	<b>0.02</b>	-5.26	9.09	0.34	0.56	-12.51	22.52	0.32	0.57	21.80	33.56	0.41	0.52
Precipitation <sup>2</sup>	-8.51	5.32	2.75	0.10	56.12	50.60	1.28	0.26	24.79	39.31	0.42	0.52	-413.30	379.73	1.15	0.28
Humidity	0.09	0.02	20.28	<b>&lt;.0001</b>	1.31	1.29	1.05	0.31	0.26	0.92	0.08	0.77	-0.13	0.28	0.22	0.64
Humidity <sup>2</sup>	-0.0007	0.0002	16.40	<b>&lt;.0001</b>	-0.0077	0.0073	1.16	0.28	-0.0021	0.0056	0.14	0.71	0.0005	0.0017	0.10	0.75

Parameter	2010 Model				2011 Model				2012 Model				2013 Model			
	Est.	SE	$\chi^2$	<i>p</i>	Est.	SE	$\chi^2$	<i>p</i>	Est.	SE	$\chi^2$	<i>p</i>	Est.	SE	$\chi^2$	<i>p</i>
Intercept	-117.59	44.49	7.54	<b>0.006</b>	-27.22	28.55	0.91	0.34	0.10	6001588	0.00	1.00	-62.17	25.29	6.26	<b>0.01</b>
Julian Date	1.42	0.42	12.67	<b>0.0004</b>	0.42	0.26	2.70	0.10	0.02	0.64	0.0006	0.98	0.67	0.27	6.32	<b>0.01</b>
Julian Date <sup>2</sup>	-0.0038	0.0011	12.91	<b>0.0003</b>	-0.0011	0.0007	2.79	0.09	0.0001	0.0017	0.0035	0.95	-0.0018	0.0007	6.02	<b>0.01</b>
Temperature	0.40	0.18	4.83	<b>0.03</b>	0.42	0.20	4.70	<b>0.03</b>	0.32	0.16	4.30	<b>0.04</b>	0.16	0.11	2.28	0.13
Temperature <sup>2</sup>	-0.03	0.01	4.38	<b>0.04</b>	-0.02	0.01	2.62	0.11	-0.02	0.01	3.02	0.08	-0.0082	0.0076	1.22	0.27
Wind Speed	0.13	0.06	6.06	<b>0.01</b>	-0.04	0.04	1.10	0.29	-0.01	0.07	0.02	0.90	-0.02	0.04	0.14	0.71
Wind Speed <sup>2</sup>	-0.0058	0.0024	6.70	<b>0.0096</b>	0.0003	0.0010	0.09	0.76	-0.0013	0.0020	0.44	0.51	-0.0002	0.0011	0.04	0.84
Precipitation	43.30	197.68	0.05	0.83	-7.99	7.27	1.22	0.27	-13.76	8.63	2.77	0.10	0.50	3.43	0.02	0.89
Precipitation <sup>2</sup>	-2017.5	15746.2	0.02	0.90	28.19	23.43	1.46	0.23	46.72	42.71	1.16	0.28	3.50	7.65	0.21	0.64
Humidity	-0.29	0.23	1.50	0.22	-0.26	0.31	0.72	0.40	-0.04	73283.8	0.00	1.00	0.01	0.02	0.52	0.47
Humidity <sup>2</sup>	0.0016	0.0014	1.21	0.27	0.0018	0.0020	0.82	0.37	-0.0001	1280.22	0.00	1.00	-0.0001	0.0003	0.06	0.80



## FIGURES

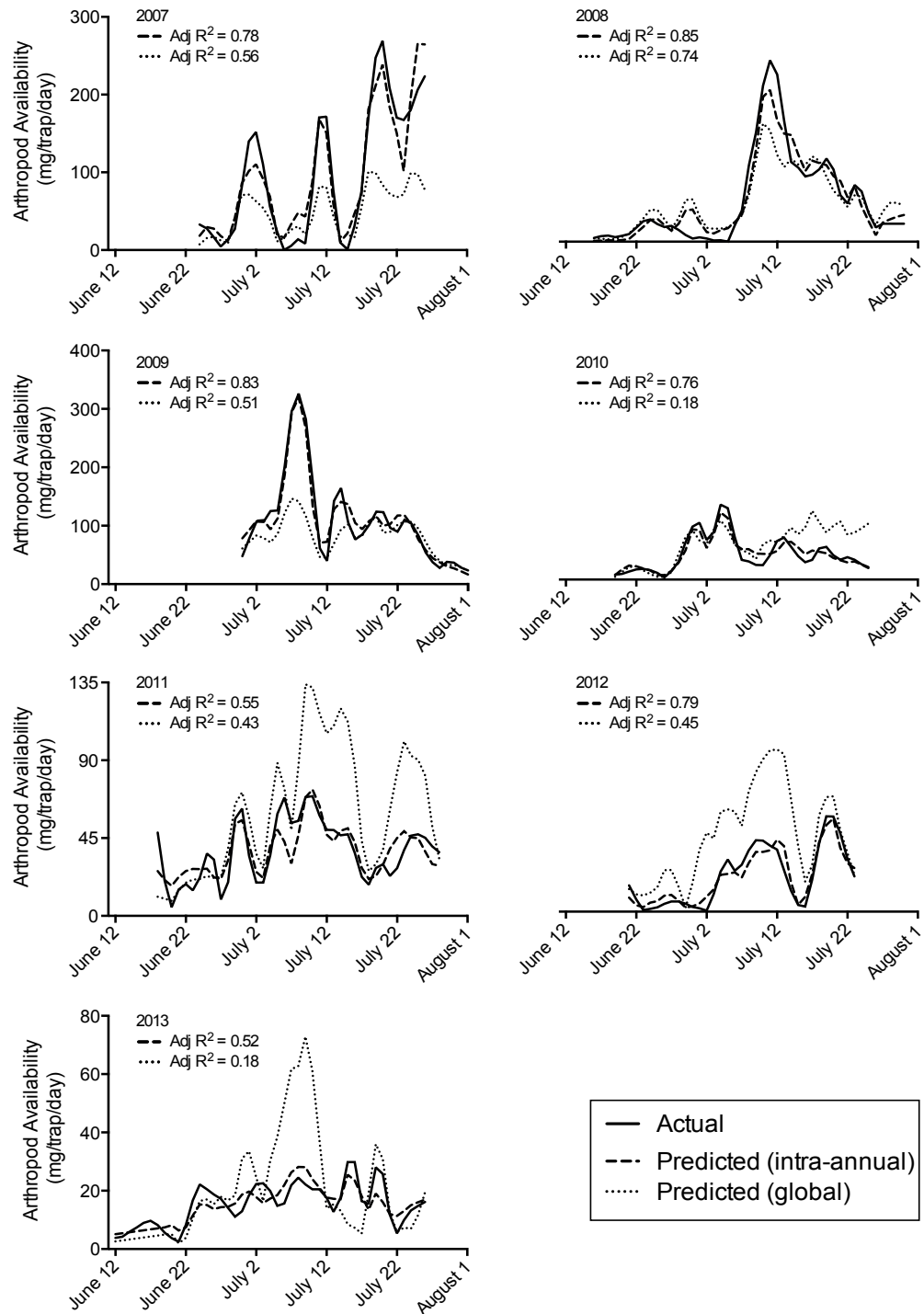


Figure 2.1 – Actual total dry arthropod biomass for 2007-2013 [solid line] and predicted arthropod biomass with their respective adjusted  $R^2$  model fit values for intra-annual models [dashed line] and global models [dotted line].

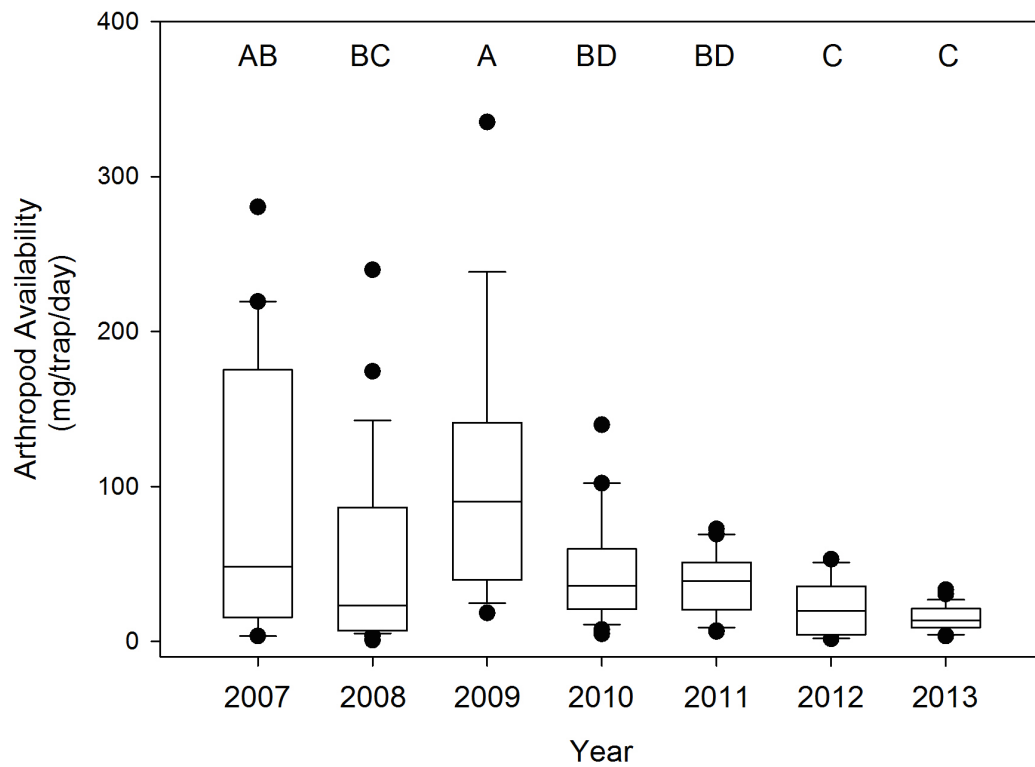


Figure 2.2 – Box plot of average arthropod biomass across 2007-2013. Letters denote which years are significantly different by Steel-Dwass test. Hinges indicate lower (25%) and upper (75%) quartile of data, band represents the median, whiskers indicate the position of the 5% quartile and 95% quartile, and dots represent outliers.

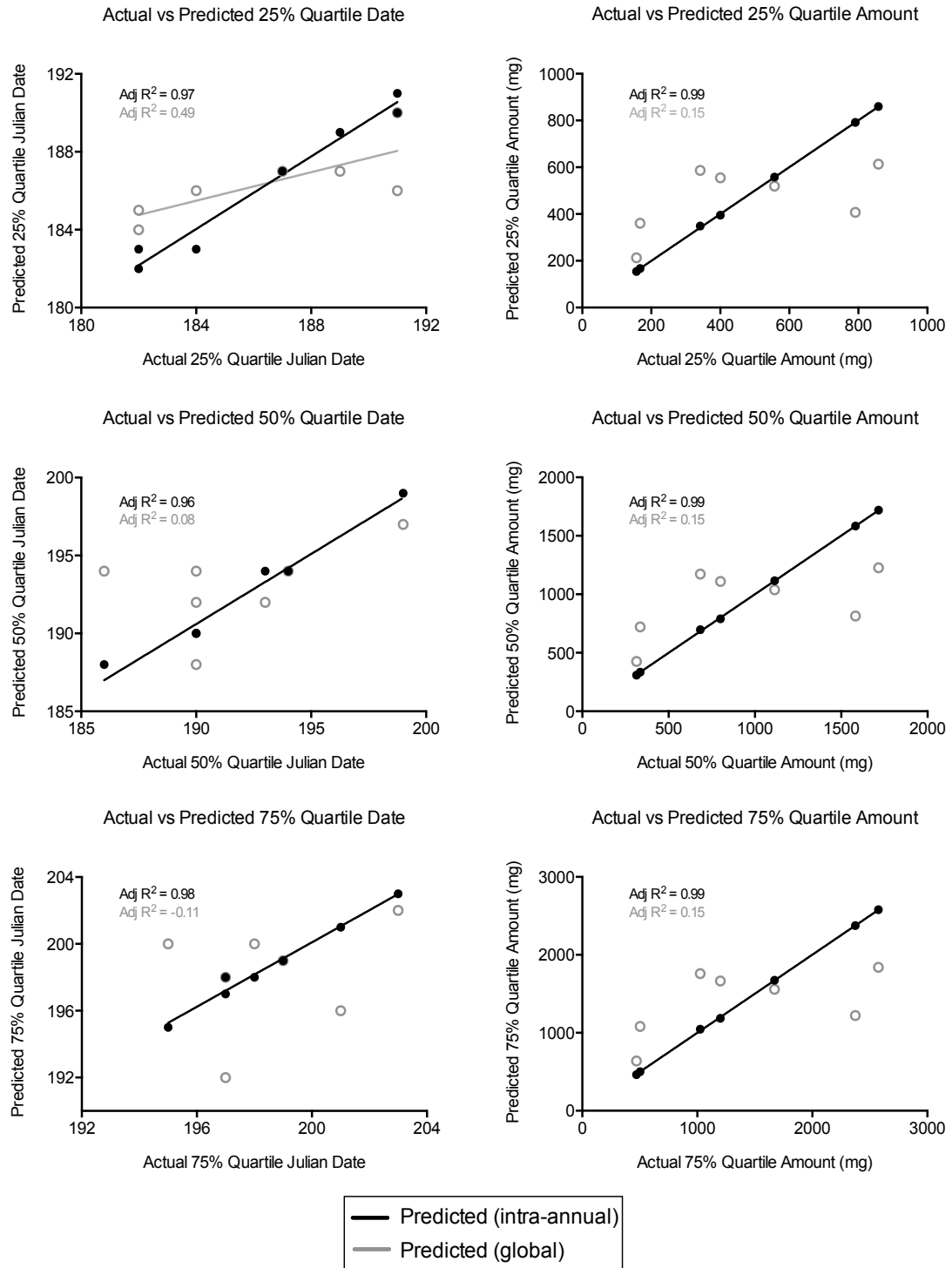


Figure 2.3 – Regression between actual quartile day and amount versus the predicted values from the intra-annual models (black) and global model (grey) with their respective adjusted  $R^2$  model fit values.

# **CHAPTER 3 – LINKING ARTHROPOD AVAILABILITY AND FITNESS IN SNOW BUNTINGS (*PLECTROPHENAX NIVALIS*)**

## **INTRODUCTION**

Phenology is the timing of life history events (e.g., migration, reproduction, and hibernation) in relation to variation in environmental factors (e.g., temperature, precipitation) (Fenner 1998, Walther *et al.* 2002, Forrest and Miller-Rushing 2010). The timing of life history events has evolved to coincide with optimal periods of resource availability to maximize fitness (Stenseth and Mysterud 2002, Varpe *et al.* 2007). Due to the finely tuned nature of these processes, a disruption in timing can have significant impacts on individual survival and/or reproductive success, and by extension, may influence ecosystems as a whole (Parmesan 2006, Forrest and Miller-Rushing 2010, Lane *et al.* 2012).

Since climatic cues can provide organisms with information of when to initiate key life history events at optimal times (Lechowicz 2002), climate change has altered the phenology and distribution of numerous species, leading to cascading changes from individuals to communities (Walther *et al.* 2002, Cotton 2003). In particular, Arctic ecosystems are facing some of the most severe and variable climatic impacts, causing numerous downstream effects on wildlife phenology, distribution, and productivity (Callaghan *et al.* 2005, Berteaux *et al.* 2006, IPCC 2007, Post *et al.* 2009, McKinnon *et al.* 2013, Legagneux *et al.* 2014). To ensure that breeding and other key life-history activities track changing climatic conditions, organisms living in these increasingly variable environments must be capable of adjusting their behavioural, physiological, or morphological phenotypes (Gaston *et al.* 2009). However, it is unknown whether Arctic-breeding species will be able to adjust quickly enough, whether all species have the same capacity to adjust and if so, by what mechanisms (Visser 2008).

Dramatic effects of phenological mismatches have been described in a number of temperate avian species, where studies have revealed that individuals that did not

advance their reproductive phenology with an advancing food supply had reduced reproductive success (Brommer *et al.* 2005; Visser *et al.* 2006). Mismatches have occurred since the major cue for many migrating birds of when to initiate migration towards breeding grounds, day length (photoperiod), is unaltered by changes in climate (Gwinner 1996, Coppack and Pulido 2004). As this cue is unable to convey climate-induced changes on the breeding grounds, birds must rely on secondary environmental cues such as temperature, which may not be a reliable indication of conditions on the breeding grounds (Coppack and Pulido 2004). A primary way in which avian reproductive success is manifested is via chick growth, health, and survival (McKinnon *et al.* 2012). For example, synchrony between offspring needs and food supply (caterpillar biomass) has been shown to impact the number of fledglings as well as fledgling weight in Dutch great tits (*Parus major*) (Visser *et al.* 2006). However, seasonal polar environments pose additional challenges for avian species that migrate long distances to breeding grounds as they must synchronize their breeding events with ephemeral peaks of resource availability during a highly constrained reproductive season (McKinnon *et al.* 2012). Furthermore, the basal food supply for insectivorous birds in the Arctic is largely composed of arthropods, which are expected to be among the most affected by rapid climatic change, as their physiology, timing of emergence, and abundance are all intimately linked to variation in ambient temperature (Høye and Forchhammer 2008, Tulp and Schekkerman 2008, Bolduc *et al.* 2013, Williams *et al.* 2015). To maximize reproductive output, hatching should occur shortly before the seasonal peak of food availability so that chicks have access to the maximum amount of resources during their period of highest demand (Visser *et al.* 2006). If reproductive phenology has not advanced to the same degree as the shifting arthropod availability, there will be less food available during chick rearing, resulting in less resources and a lower chick survival and fledging success (Thomas *et al.* 2001, Both *et al.* 2005, McKinnon *et al.* 2012).

While the fitness impacts of climate change on investment decisions manifest themselves largely via changes in laying phenology (i.e., date at which egg laying is initiated), some temperate species also have the capacity to alter decisions such as clutch size, laying interval, incubation period, or the number of broods within a season (Cresswell and McCleery 2003, Visser *et al.* 2003). Unfortunately, comparatively little is

known regarding the mechanisms linking climatic variation and fitness in Arctic-breeding insectivorous birds, despite the likelihood of these species being at greatest risk of phenological mismatches (Pearce-Higgins *et al.* 2005, Tulp and Shekherman 2008). Importantly, Arctic-breeding songbirds are expected to have a lower capacity for phenological flexibility as the short growing season of the Arctic constrains optimal periods of breeding and typically limits species to a single reproductive event per year (Martin and Wiebe 2004).

Here we examine the potential impact of a phenological mismatch between an Arctic-breeding passerine (snow buntings, *Plectrophenax nivalis*) and their prey items using a seven-year dataset that includes arthropod abundance, avian reproductive measures, and climate data collected in the low Canadian Arctic. Specifically, we investigated whether 1) reproductive period, investment, and success varied across sampling years for the population of snow buntings, 2) early climatic conditions influenced the phenology of snow buntings and their food source, 3) arthropod abundance during the offspring provisioning period varied across sampling years, 4) arthropod abundance over the entire breeding season or during the peak of offspring provisioning influenced reproductive success at the population and individual level, and 5) the timing of arthropod emergence and the degree to which snow bunting hatch date corresponds to the maximum arthropod abundance influences reproductive success of individuals. We predicted that early season temperature and lay date (and by association hatch date) would be negatively correlated, as resources are scarcer in colder conditions leading to a delay in the initiation of breeding. We also predicted that reproductive success at both the individual and population level would be positively correlated with arthropod abundance during the chick-rearing period, as greater food availability should provide a higher survival rate among chicks. Lastly, we predicted that reproductive success would be higher in individuals that have best timed their hatch date to coincide with optimal food availability.

## **METHODS**

### **Study Species and Reproductive Monitoring**

Snow buntings are a circumpolar, Arctic-breeding passerine that time their spring migration to the Arctic with the onset of snowmelt because their diet comprises of insects, which reside in snow free areas (Montgomerie and Lyon 2011). Females produce a single clutch per season of 5 to 7 eggs on average (Montgomerie and Lyon 2011). As income-breeders, the resources used for reproductive activities are acquired solely on the breeding grounds (Moltofte *et al.* 2007). Both parents feed nestlings arthropods, predominantly from the order *Diptera* (flies) (Parmelee 1968). Data from the Christmas Bird Count indicate that North American populations have declined approximately 64% in the past 40 years (Butcher and Niven 2007). A focal breeding population of snow buntings has been studied at East Bay (Mitivik) Island since 2007 (Macdonald *et al.* 2012, Guindre-Parker *et al.* 2013, Baldo *et al.* 2014). This population is ideal for reproductive monitoring for a number of reasons: 1) high breeding density due to the availability of nest sites, 2) the presence of multiple feeding ponds from which arthropods emerge, 3) a lack of mammalian predators, and 4) the island's small size allowing for the monitoring of all individuals. Birds are captured from the period of migratory arrival beginning in late May until breeding in early-mid June using Potter traps baited with mixed finch seed. Following capture, pair identities are confirmed, and nests are located and visited regularly every 2-3 days to determine the start of laying (i.e., laying date), clutch size, and hatching date. In instances where lay date was known but not hatch date (or vice versa), the unknown date was calculated by using the mean incubation period of the colony (10.5 days) and clutch size (with the knowledge that only 1 egg is laid per day). Nest-bound juveniles are banded before leaving the nest at approximately 8 days of age, and the number of nestlings at this time serves as a measure of reproductive output.

### **Arthropod Sampling and Quantification**

Arthropod sampling was conducted at two sites: East Bay mainland site (2007 and 2008) and East Bay (Mitivik) Island site (2009-2013). These two sites are significantly correlated in arthropod abundance (Appendix A). Samples were collected using passive

modified pitfall traps (as outlined in Bolduc *et al.* 2013). Traps are composed of a square containing a fine mesh placed upright directly over a plastic pitfall trough. An inverted plastic cone surrounding the mesh funnels flying insects up to a collection bottle. The trap captures ground-dwelling arthropods which fall directly into the pitfall as well as low-flying arthropods, which hit the mesh, and either fall into the trough or climb to the collection bottle. Capture totals from modified pitfall traps incorporate both density and activity levels of surface-dwelling arthropods, and can therefore be used as a reliable proxy for arthropod availability at sampling sites (Southwood and Henderson 2000). Sampling periods were chosen to coincide with migrating passerine and shorebird arrival/breeding dates from early June to late July in each year. Collection at the mainland site was conducted in low wetland tundra (2007 – 5 traps, 2008 – 3 traps) and at the island site in low wetland tundra adjacent to 2 small ponds, Camera pond and Nanook pond (2009-2013 – 4-8 traps). These 2 pond sampling locations are significantly correlated in arthropod abundance (Appendix B). Traps were visited every two days, and samples were collected and stored in ethanol (70%) until quantification and identification in the laboratory. Arthropods were sorted to order with true spiders (*Araneae*) grouped together, and springtails (*Colembola*) and mites (*Acari*) excluded due to their negligible contribution to overall biomass. Each order from samples from 2009-2013 were dried in pre-weighed paper envelopes at 50°C for 5 days and weighed using an electronic balance to the nearest 0.01mg. Dry biomass values for samples from 2007 and 2008 were obtained by converting arthropod counts using length to dry mass equations (McKinnon *et al.* 2012, Bolduc *et al.* 2013). Biomass totals for all arthropods collected were determined and arthropod availability was calculated by dividing total arthropod biomass by the number of traps sampled and by the number of days between changing the collection vessel. Therefore, all arthropod availability measures are presented in mg/trap/day.

## **Climatic Data**

We used data collected by Environment Canada at the Coral Harbour weather station, Nunavut (64°110 N, 83°210 W - located 50km from the focal study site) to



represent local climatic conditions prior to the breeding period of the snow bunting population on East Bay Island.

## **Statistical Analyses**

### ***Inter-annual Breeding Patterns***

Number of fledglings has been proposed to be the factor most correlated with lifetime fitness of passerine species (McCleery *et al.* 2004, Williams 2012) and thus we use this metric as an indication of reproductive success for our population of snow buntings. First, we investigated inter-annual differences in adult female snow bunting reproductive timing, investment, and success by comparing average hatch date, clutch size, and number of fledglings, respectively, between years. For individual females that were recaptured across years (4 individuals in total), only one entry was kept at random to prevent pseudo-replication. Laying date and hatching date are highly correlated in this population (Guindre-Parker *et al.* 2013). As such, even though female buntings are making the “decision” of when to breed via laying date, we use hatch date throughout this chapter since it is the reproductive decision being acted upon by selection via its relative timing with arthropod emergence. As hatch date values were normal, but had unequal variances by Levene’s test, a Welch’s test with a Games-Howell post-hoc was used in SPSS to investigate differences in hatch date across years. Clutch size values were found to be non-normal and were not improved with transformation, thus a Kruskal-Wallis test with a Steel-Dwass post-hoc was used to investigate investment differences across years. Number of fledglings was squared in order to achieve normality. Because transformed values had equal variances by Levene’s test, an ANOVA with a Tukey post-hoc test was used to investigate differences in reproductive success across years.

### ***Influence of Early Climatic Conditions on Food Resources and Reproductive Timing***

As Arctic habitats are constrained by climate, the effect of late spring climate on both arthropod emergence and snow bunting reproductive timing in the 7 study years was assessed using mean temperature in late May (i.e., spring climate). Mean daily temperature was extracted for the month of May from 2007-2013 and the mean temperature of late May (May 15<sup>th</sup> -31<sup>st</sup>) was calculated for every year. We used a linear

model with mean temperature of late May as the independent variable and average hatch date as the dependent. A separate linear model was created with mean temperature of late May as the independent variable and the Julian date of the 50% quartile of arthropod abundance as the dependent variable to examine whether early temperature influences arthropod emergence. Both hatch date and date of the 50% quartile of arthropod abundance were normal without transformation.

### ***Inter-annual Arthropod Abundance Patterns***

Total seasonal arthropod abundance was previously shown to significantly differ between years (Marier 2015, Chapter 2). However, as arthropods at this location do not show a defined peak in abundance (Marier 2015, Chapter 2 – see Figure 2.1), this overall pattern may be of little importance to snow buntings if this abundance does not occur during periods of high food demand. Therefore, to determine inter-annual differences in the availability of food during a time period that is biologically-relevant to snow bunting reproduction, the cumulative abundance of arthropods from hatch date to fledge date (9 days total) was calculated for each nest. As abundance during chick provisioning could not be normalized within all years, a Kruskal-Wallis test with a Steel-Dwass post-hoc was used to investigate differences across years.

### ***Relationship Between Food Abundance and Reproductive Success***

To further examine a possible mechanism for variation in reproductive success, we investigated the importance of arthropod abundance during both the entire season and the more biologically-relevant nestling provisioning period to the reproductive success of snow buntings at both the population and individual level. We also included hatch date in these models due to the known influence of reproductive timing on fledgling success in Arctic systems. First, to determine the impact of total seasonal arthropod biomass and hatch date on reproductive output at the population level, we used a multiple regression approach with total seasonal arthropod biomass and average hatch date as independent variables and the number of fledglings as the dependent variable. Next, to increase biological-relevance, a multiple regression approach was again conducted at the population level but with seasonal average arthropod biomass during the 9 days of chick

provisioning and hatch date as the independent variables. Finally, the impact of arthropod biomass during the 9 days of chick provisioning was investigated at the individual scale. A generalized linear mixed model (GLMM) with a Poisson distribution and log link function was created with the cumulative arthropod biomass from hatch to fledge as the independent variable and hatch date as a fixed effect. The dependent variable was again number of fledglings and year was included as a random effect.

### ***Effect of Synchronization of Breeding and Food Availability on Reproductive Success***

While the previous analysis incorporated the timing of arthropod emergence to some extent (due to the use of arthropod abundance during a key reproductive time period) we wanted to further assess the importance of timing reproduction to an optimal period of food availability. However, as mentioned previously, it is difficult to identify peak food availability at this site, as the arthropods do not show a pronounced peak in abundance. Additionally, the variation and lack of obvious peak means that “days from maximum abundance” is not a useful measure of timing. Instead, we calculated two separate measures of arthropod timing by subtracting an individual female snow bunting’s realized amount of arthropods during the 9 day offspring provisioning period from either the maximum 9-day cumulative arthropod biomass for a given year (peak 9-day window), or the cumulative 9 day abundance surrounding the 50% quartile date of the total seasonal arthropod biomass (the abundance on the 50% quartile date, as well as that of the 4 days prior and following it). As total arthropod biomass varied by an order of magnitude between years (Marier 2015 Chapter 2; Figure 2.1; Table 2.1) and the maximum possible reproductive success was expected to be different in years that differed greatly in total abundance, data from each year was separated into 3 categories based on total abundance: high abundance (2007-2009), moderate abundance (2010-2011), and low abundance (2012-2013). To assess the importance of timing reproduction to a period of high arthropod abundance, we ran a generalized linear model with a Poisson distribution and log link function with number of fledglings as the dependent variable, a measure of arthropod abundance from the maximum as the independent, and arthropod abundance category as a fixed effect. All statistical analyses were conducted in JMP 12 unless otherwise noted.

## **RESULTS**

### **Inter-annual Variation in Breeding Patterns**

Lay date, clutch size, and number of fledglings varied considerably between 2007-2013 (Table 3.1). Hatch date was significantly different among years (Welch's:  $F=29.24$ ,  $df=6$ ,  $p<0.0001$ ; Fig 3.1-A). There were also significant differences in clutch size across years (Kruskal-Wallis:  $\chi^2=21.33$ ,  $df=6$ ,  $p=0.0016$ ; Fig 3.1-B) and the number of fledglings was also significantly different among years (ANOVA:  $F=5.07$ ,  $df=6$ ,  $p=0.0002$ ; Fig 3.1-C).

### **Influence of Early Climatic Conditions on Food Resources and Reproductive Timing**

Snow buntings laid earlier in warmer years as late May (May 15<sup>th</sup> – 31<sup>st</sup>) mean temperature was significantly negatively correlated with mean hatch date between 2007-2013 (Linear model:  $F=13.46$ ,  $df=6$ ,  $p=0.0145$ ; Figure 3.2-A). However, counter to our prediction, late May mean temperature did not predict arthropod emergence, as it was not significantly correlated with the 50% quartile date of arthropod abundance (Linear model:  $F=0.94$ ,  $df=6$ ,  $p=0.377$ ; Figure 3.2-B).

### **Inter-annual Arthropod Abundance Patterns**

Similar to findings for total arthropod biomass in Chapter 2, arthropod biomass during offspring provisioning (9 days from hatch to fledge) was significantly different between years (Kruskal-Wallis:  $\chi^2=67.18$ ,  $df=6$ ,  $p<0.0001$ ; Figure 3.3).

### **Relationship Between Food Abundance and Reproductive Success**

At the population level, the mean number of fledglings was not significantly correlated with total arthropod biomass during each sampled year (Multiple Regression:  $F=0.93$ ,  $df=6$ ,  $p=0.466$ ; Figure 3.4-A). The mean number of fledglings was also not significantly correlated with the mean arthropod abundance during offspring provisioning

(9 days from hatching to fledging) (Multiple Regression:  $F = 6.03$ ,  $df = 2$ ,  $p = 0.062$ ; Figure 3.4-B). However, the number of fledglings produced by individual snow buntings was positively correlated with arthropod abundance during offspring provisioning (Est.=0.0003, S.E.=0.001,  $\chi^2 = 6.72$ ,  $p = 0.0096$ ; Fig. 3.4-C) and hatch date (Est.=-0.037, S.E.=0.018,  $\chi^2 = 4.45$ ,  $p = 0.035$ ; Overall GLMM:  $\chi^2 = 10.45$ ,  $df = 2$ ,  $n = 78$ ,  $p = 0.0054$ ).

## **Effect of Synchronization of Breeding and Food Availability on Reproductive Success**

The number of fledglings produced by individuals was significantly related to the difference between actual arthropod biomass during the 9 days of offspring provisioning and the maximum seasonal 9 day biomass when categorized by total abundance (high years (2007-2009), moderate years (2010-2011), and low years (2012-2013); GLM:  $\chi^2 = 10.40$ ,  $df = 3$ ,  $p = 0.0155$ ; Figure 3.5-A, Table 3.2). Snow buntings fledged more offspring in years with high total biomass when compared to those of low biomass (Figure 3.5-A, Table 3.2). However, there was no correlation between the number of fledglings and the difference in arthropod biomass during offspring provisioning and in the biomass of the 9 days surrounding the 50% quartile of seasonal abundance (GLM:  $\chi^2 = 6.03$ ,  $df = 3$ ,  $p = 0.1104$ ; Figure 3.5-B).

## **DISCUSSION**

### **Inter-annual Breeding Patterns and the Influence of Early Climatic Conditions on Food Resources and Reproductive Timing**

In a seven-year dataset from the low Canadian Arctic, snow bunting reproductive timing varied significantly from year to year. Furthermore, hatch date was negatively correlated to colder temperatures in late May indicating that warmer pre-laying temperatures were associated with earlier initiation of reproduction (i.e., laying date) and therefore hatch dates. This observed relationship with warmer temperature and an earlier initiation of reproduction has been observed in a multitude of studies (Dunn 2004 and references therein). This result highlights the potential for environmental constraints to act on reproductive decisions in the Arctic, where the temporal occurrence of the

sequence of avian reproductive events (gamete production, laying, incubation, hatching, and offspring provisioning) is influenced by early seasonal conditions (Eeva *et al.* 2000). Furthermore, given that arrival phenology has remained relatively inflexible from 2007-2013 and occurs between the last week of May and the first week of June (Mckinnon *et al. submitted*), this suggests overall that snow buntings may not be able to adjust their reproductive timing based on spring climatic cues, but rather may be constrained to initiate reproduction at the earliest possible permissible conditions (i.e. sufficient food supply) (Drent 2006).

We also found significant differences in clutch size among years, which may be a result of factors influencing the resource-gathering potential of individuals, such as environmental conditions and food availability (Hussell 1972). As such, the fewer resources available during egg production, the less energy that is available for investment in gamete production, which can ultimately lead to a smaller brood size (Kunz and Orrell 2004). Reasons for clutch size differences were not tested here, as early (pre-laying) season sampling of arthropods was not possible. Additionally, male snow buntings feed females during incubation and it has been found that there is considerable variation in incubation feeding frequency among males (Lyon *et al.* 1987). Thus, mate choice becomes a critical component in the amount of arthropods foraged, ultimately determining the energy budget of females during incubation, and ultimately hatching success. Furthermore, the individual optimization hypothesis (Perrins and Moss 1975) poses that each female should be able to adjust her clutch size to match her circumstances (such as body condition, quality, food availability) to maximize her fitness (Williams 2012). Lastly, there were significant differences in reproductive output across years. While incubation feeding likely had influences on this outcome (Lyon and Montgomerie 1985), we sought to examine resource availability during chick provisioning as a potential explanation of this variation (see below).

### **Inter-annual Arthropod Abundance Patterns**

When comparing the cumulative abundance of arthropods during the offspring-provisioning period for individual snow buntings, we found significant differences

among the 7 sampled years. Interestingly, the inter-annual differences in arthropod biomass during chick provisioning are different from the pattern in the total amount of arthropods (Marier 2015, Chapter 2 – see Figure 3.3). This suggests that a year characterized by low arthropod abundance across the entire season does not necessarily mean that individual snow buntings will be unable to acquire sufficient resources during the peak of offspring demand. Increased foraging rates could compensate in years of low abundance. Therefore, there does not appear to be a strict relationship between total arthropod abundance and arthropod abundance during an integral window during reproduction. This is important for snow buntings as even in years of low arthropod abundance, there are periods during the season that allow for successful offspring provisioning. Overall, the variation exhibited in arthropod abundance and emergence across years is highly influenced by varying climate conditions and is likely to continue to become variable as climate change worsens (Chapter 2).

### **Relationship Between Food Abundance and Reproductive Success**

Mean snow bunting reproductive output for the population was not significantly related to the total abundance of arthropods during the season or to the abundance during the average chick provisioning period. However, at the individual level, reproductive output was positively related to the abundance of arthropods during the chick-provisioning period. Specifically, individuals raising chicks at time periods with higher insect biomass were able to fledge a greater number of offspring. Taken together, these findings suggest that it is not the absolute abundance of resources during the entire season that will significantly impact reproductive success, but rather the arthropod abundance during key periods of time, such as when offspring demand is at its peak. Because the period of offspring provisioning (determined by hatch date) will have a crucial impact on number of fledglings, and reproductive timing (i.e. hatch date) has been shown to be constrained by temperature, variation in climate may have a large downstream effect on reproductive success of individuals. The existence of a relationship at the individual level but not at the population level may be due to a comparatively small sample size ( $n=82$  for individuals vs  $n=7$  for population) and further years of analyses may elucidate population-level patterns. However, the lack of relationship for the population is likely at

least partly due to the inherently large variation in individual performance, such as offspring provisioning (where a high degree of individual variation in provisioning rates have been observed across many different avian taxa) (Williams 2012). Variation in individual performance may be attributed to quality and/or age (Ardia and Clotfelter 2007). For example, a study in tree swallows (*Tachycineta bicolor*) found that when faced with a handicap during the reproductive season, older females suffered self-maintenance costs but raised offspring in good condition while younger females produced offspring in poor condition and invested more into self-maintenance (Ardia and Clotfelter 2007). Thus, the age of an individual may be a major determinant in the amount of investment allocated to offspring, where younger, inexperienced females may focus more on survival than reproductive output (Forslund and Part 1995, Kunz and Orrell 2004, Ardia and Clotfelter 2007). Additionally, male contribution to nestling provisioning has been found to be central to offspring quality and survival in snow bunting chicks, particularly in years with lower food abundance (Lyon *et al.* 1987), thus male performance becomes a crucial factor in the success of offspring provisioning (Butcher and Niven 2007).

## **Effect of Synchronization of Breeding and Food Availability on Reproductive Success**

The reproductive output of individual snow buntings was highest when the abundance of arthropods during their specific chick-provisioning period was closest to the period of maximum arthropod abundance for the year. Interestingly, individuals in years of higher relative arthropod abundance (e.g., 2007-2009) fledged approximately the same number of offspring when mismatched with the maximum period than perfectly-matched individuals in years of lower abundance (2012-2013). This result further supports the interaction between arthropod timing and abundance and individual timing for influencing bunting reproductive output. We found no significant effect of mistiming on reproductive output when we examined the period surrounding the midpoint of arthropod emergence (50% quartile date). This highlights the nature of arthropod availability in the Arctic; availability is not a constant progression to a peak followed by a decline, but instead is highly variable, oftentimes with no clear peak. Thus, a mismatch



with the midpoint of abundance during the season may not be as important to snow bunting reproductive success as noted in temperate species (Visser *et al.* 2006).

## **Conclusion**

While climate change is causing pronounced ecological changes worldwide, its effects on a particular species or population can be indirect, influencing factors such as phenology that eventually manifest themselves in a cascading manner (Walther *et al.* 2002, Post *et al.* 2009). Our study demonstrates that fluctuating climatic conditions in the Arctic may constrain the reproductive phenology of snow buntings and are not similarly constraining the emergence of their required food resource, arthropods. In addition, arthropod availability, and snow bunting reproductive timing, investment, and output were found to be significantly variable inter-annually. Resource abundance during offspring provisioning was found to be a significant factor in the reproductive output of individuals. Furthermore, the degree of match between resource availability during an individual's offspring provisioning period and the maximum period of resource availability was the best resource-based predictor of reproductive success. Therefore, snow buntings may be susceptible to the effects of climate change as at the population level climate is differentially affecting their phenology and that of their prey items. Further studies into the degree of individual flexibility in breeding phenology in this species and the impact of this flexibility on reproductive output (i.e., reaction-norm analyses, Brommer *et al.* 2005) will help to determine whether enough individuals can adjust breeding decisions to match resource availability to sustain populations.

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## TABLES

Table 3.1 – Inter-annual variation in lay date, clutch size, and number of fledglings for snow buntings (*Plectrophenax nivalis*) breeding at East Bay Island, Nunavut between 2007-2013.

Year	Lay date					Clutch Size					# Fledglings				
	n	Min	Max	Mean	SE	n	Min	Max	Mean	SE	n	Min	Max	Mean	SE
2007	11	172	177	174.55	0.39	6	2	6	4.67	0.84	11	0	4	2.27	0.45
2008	18	166	171	167.61	0.39	19	4	7	6.00	0.19	19	0	5	3.58	0.38
2009	15	170	178	172.40	0.47	14	5	6	5.64	0.13	12	3	6	4.92	0.26
2010	17	163	173	168.24	0.78	17	5	7	5.94	0.16	15	0	5	3.80	0.38
2011	13	167	175	171.08	0.60	12	5	8	5.94	0.30	12	0	6	3.83	0.55
2012	9	172	180	175.89	0.95	12	2	7	4.67	0.40	12	0	5	2.50	0.53
2013	12	170	179	174.25	0.72	14	3	6	4.93	0.22	14	0	5	3.29	0.46

Table 3.2 – Generalized linear model for analysis of effect of difference in actual 9 day offspring provisioning arthropod biomass from maximum seasonal 9 day arthropod biomass on reproductive success across three categories of total abundance.

Term	Est.	SE	$\chi^2$	<i>p</i>
Intercept	1.4191	0.0772	231.35	<b>&lt;0.0001</b>
Low Abundance*	0.2579	0.1023	6.08	<b>0.0137</b>
Moderate Abundance*	0.0139	0.0883	0.02	0.8745
Mismatch from Maximum Arthropod Biomass	-0.0005	0.0002	8.02	<b>0.0046</b>

\* in reference to High Abundance Category



## FIGURES

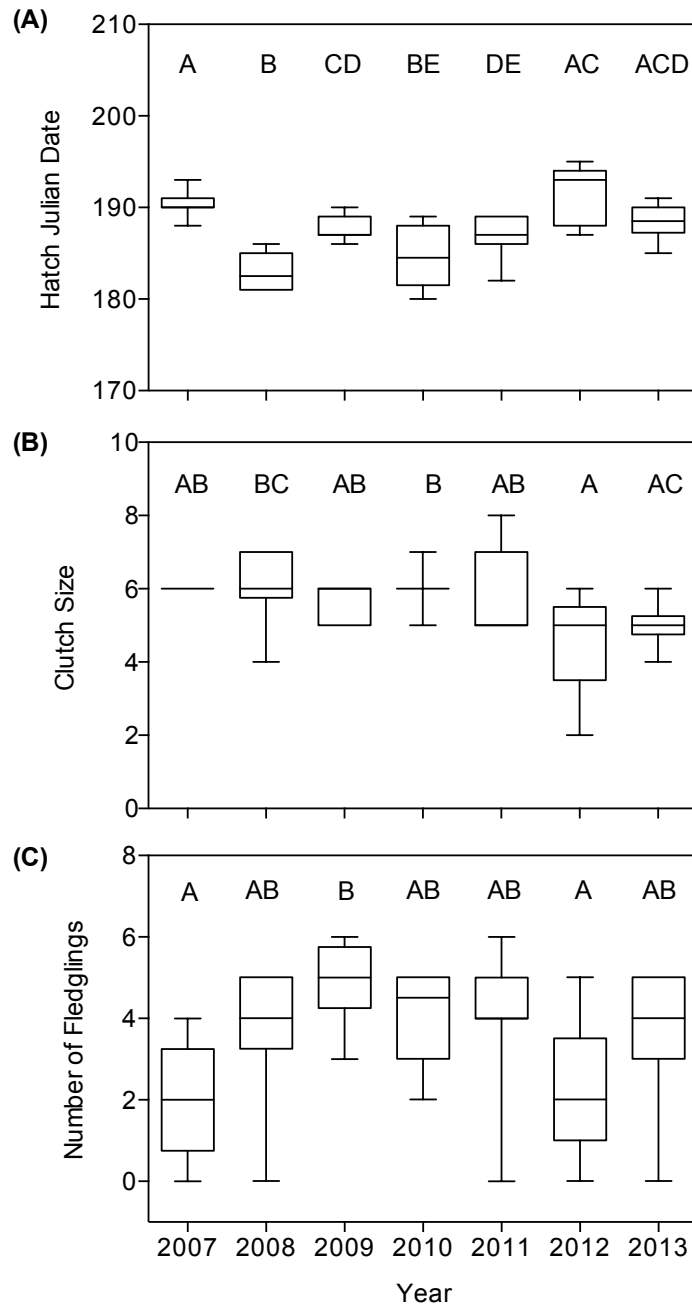


Figure 3.1 – Box plot of (A) average hatch date ( $F = 29.24$ ,  $df = 6$ ,  $p = <0.001$ ), (B) average clutch size ( $\chi^2 = 21.33$ ,  $df = 6$ ,  $p = 0.0016$ ), and (C) average number of fledglings ( $F = 5.07$ ,  $df = 6$ ,  $p = 0.0002$ ) across 2007-2013. Letters denote years that are significantly different at  $p = 0.05$ . Hinges indicate lower (25%) and upper (75%) quartile of data, the band represents the median, and whiskers indicate the position of the 5% quartile and 95% quartile.

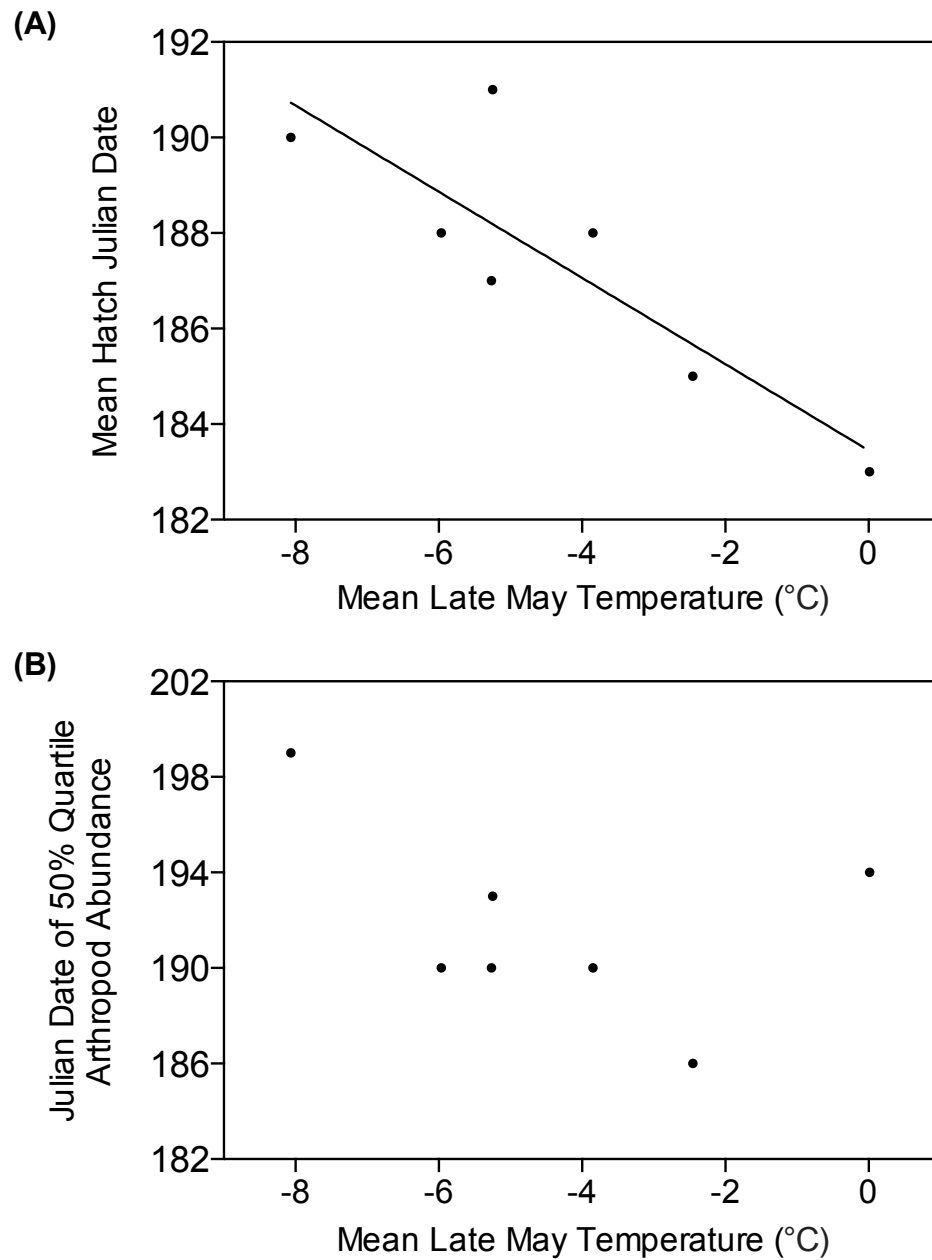


Figure 3.2 – Regression of mean temperature in late May (May 15-31) with (A) mean hatch date of snow buntings ( $F=13.46$ ,  $df=6$ ,  $p=0.0145$ ) and (B) date of 50% quartile arthropod abundance ( $F=0.94$ ,  $df=6$ ,  $p=0.38$ ).

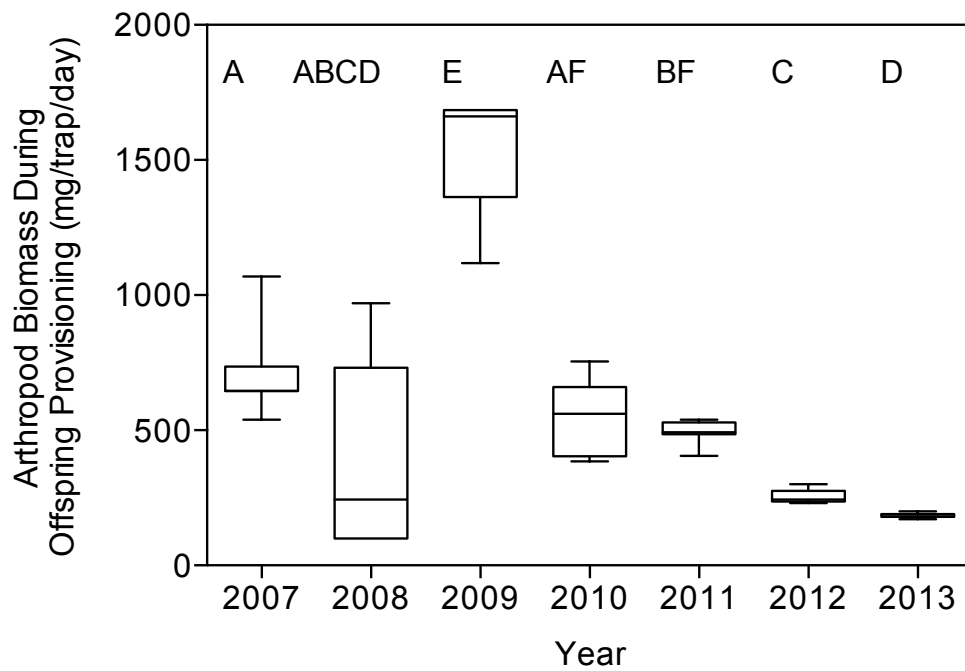


Figure 3.3 – Box plot of average arthropod biomass during offspring provisioning ( $\chi^2=67.18$ ,  $df=6$ ,  $p<0.0001$ ). Letters denote years that are significantly different at  $p=0.05$ . Hinges indicate lower (25%) and upper (75%) quartile of data, the band represents the median, and whiskers indicate the position of the 5% quartile and 95% quartile.

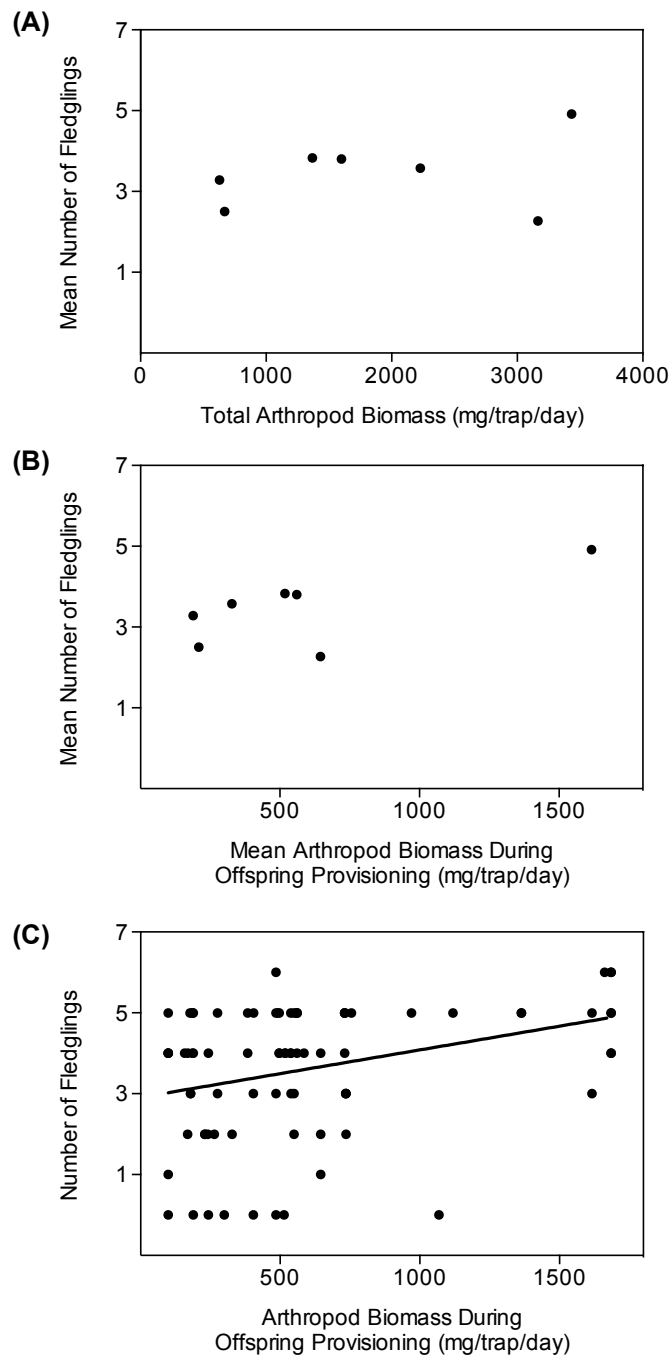


Figure 3.4 – Relationship between the mean number of fledglings and (A) total arthropod biomass (GLM;  $F = 0.93$ ,  $df = 6$ ,  $p = 0.47$ ), (B) mean arthropod biomass during offspring provisioning (GLM;  $F = 6.03$ ,  $df = 6$ ,  $p = 0.062$ ), and (C) arthropod biomass during offspring provisioning (GLMM:  $\chi^2 = 10.45$ ,  $df = 2$ ,  $n = 78$ ,  $p = 0.0054$ ).

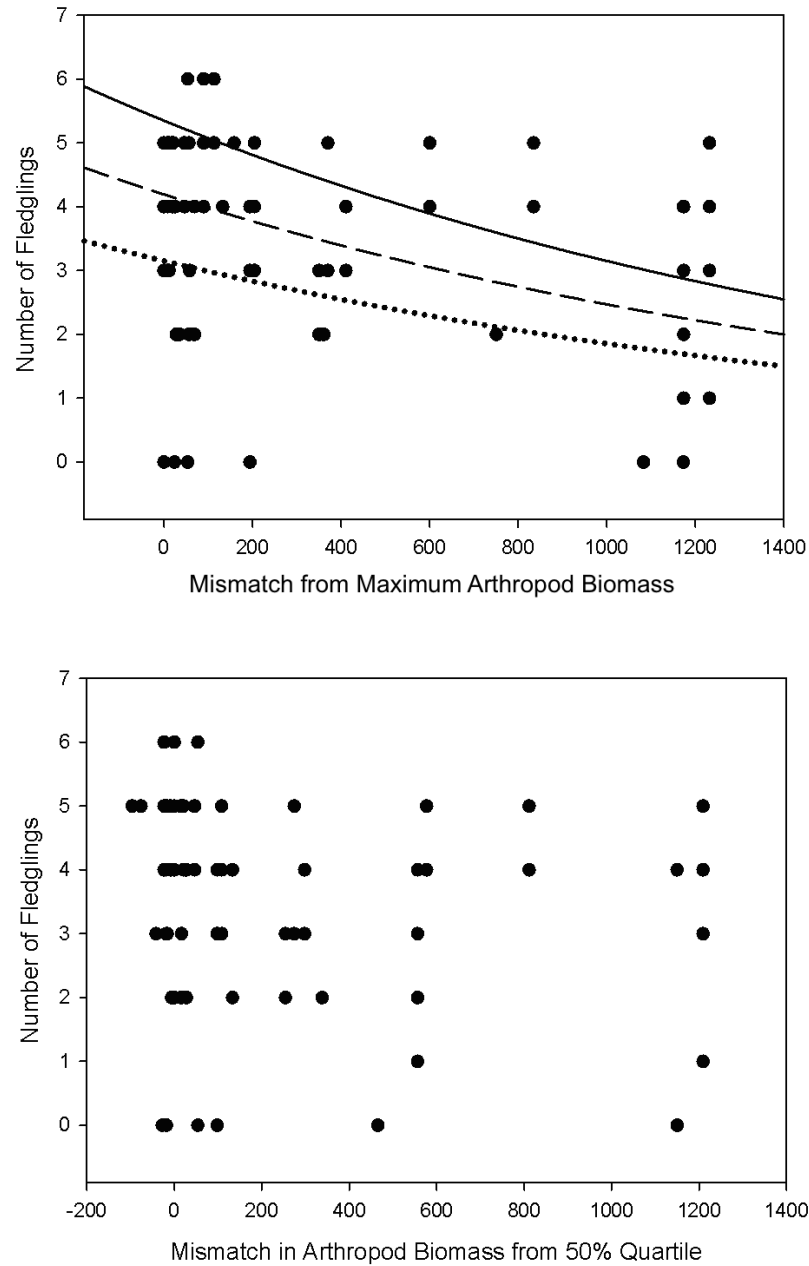


Figure 3.5 – Relationship between the number of fledglings and (A) the difference in arthropod biomass during offspring provisioning from maximum amount of biomass possible during high years (2007-2009; solid line), moderate years (2010-2011; dashed line), and low years (2012-2013; dotted line) (GLM;  $\chi^2 = 10.40$ ,  $df = 3$ ,  $p = 0.0155$ ) and (B) the difference in arthropod biomass during offspring provisioning from the amount at the 50% abundance quartile (GLM;  $\chi^2 = 6.03$ ,  $df = 3$ ,  $p = 0.1104$ ).

## CHAPTER 4 – GENERAL DISCUSSION

### SUMMARY AND IMPLICATIONS OF FINDINGS

The overall goal of this thesis was to examine how climatic variation is impacting the emergence and abundance of Arctic arthropods and if an Arctic passerine's reproductive success is influenced by their ability to synchronize their breeding to ephemeral arthropod availability. As ecological impacts from climate change are more pronounced in these regions (Parmesan 2006, Post *et al.* 2009), it is important to understand how species breeding in these highly variable environments are responding to climate change and how they will fare in the future (McKinnon *et al.* 2012).

The second chapter examined the effectiveness and potential limitations of climate-based predictive modeling of Arctic arthropod distributions by comparing two different climate-based modeling approaches. We first discovered that in contrast to theoretical arthropod phenology models (Visser *et al.* 2006), no clear 'peak' of arthropod abundance could be discerned within years at this and other Arctic sites (Bolduc *et al.* 2013). Instead, we determined that calculated quartile values may be a more objective means of quantifying arthropod timing and abundance, especially when being used to predict potential phenological match/mismatches with avian predators. Secondly, while all intra-annual models yielded significant predictive capacity, the individual climatic variables that significantly predicted arthropod emergence patterns varied widely across years. For example, temperature, which has previously been shown to be a major regulating factor in arthropod phenology (Høye and Forchhammer 2008, Tulp and Schekkerman 2008, Williams *et al.* 2015), did not contribute significantly in all model years. We proposed that this large inter-annual variability in climatic influence on arthropods to be a major factor surrounding the variability in the predictive capacity (adjusted  $R^2$  model fits = 0.52 to 0.85) of intra-annual models across years. Finally, by constructing an inter-annual model we then evaluated whether a single, global climatic model could be used to accurately predict arthropod phenology and abundance. If significant and accurate, such a model would be highly useful in hind- or fore-casting arthropod availability in previous or future years where arthropods were not directly

sampled, respectively. Although significant, the global model predicted arthropod availability with far less accuracy than any of the intra-annual models. We proposed this to be a result of the high variability in whether a given climatic variable was significant within a given intra-annual model, leading to inaccurate predictions of abundance. The contrast of predictive power between these intra- and inter-annual models suggests that there may be additional factors other than climate contributing to the intra-annual variability in arthropod phenology and abundance. Unfortunately, we therefore caution the use of ‘simplistic’ climate-only approaches to predict Arctic arthropod emergence patterns.

The third chapter examines direct and indirect linkages between climatic variation, arthropod timing and abundance, and snow bunting breeding productivity. Importantly, we took both a population- and individual-level approach to examine the fitness consequences incurred from timing bunting reproduction to match resource availability. As noted above, previous temperate studies have attempted to link an assumed peak of arthropod abundance to avian reproductive success within a match/mismatch framework (Cresswell and McCleery 2003, Visser *et al.* 2004, Visser *et al.* 2006, McKinnon *et al.* 2012). To test this match/mismatch hypothesis robustly in a highly variable Arctic environment, we extracted arthropod abundance metrics as they relate to a biologically relevant period for snow buntings (i.e., the period when nestling demand is greatest), and then compared how well this predicted snow bunting productivity versus a single ‘peak’ of abundance approach. At the population level, snow bunting laying decisions were highly constrained by spring (late May) temperatures, with colder springs resulting in significantly later mean laying dates. Perhaps not surprisingly, overall breeding productivity was higher in years of higher arthropod abundance. At the population level, abundance during this biologically-relevant period was a significant positive predictor of bunting breeding productivity; the ‘peak’ abundance approach showed no such relationship. At the individual level, female buntings that timed laying to temporally match peak nestling demand and arthropod abundance had the highest reproductive success, even within low arthropod abundance years. These results first indicate that bunting breeding decisions and productivity are both directly constrained by, and indirectly linked to climate, mediated directly in the latter via impacts of arthropod

emergence patterns on the number of offspring fledged. Overall, while it does not appear that buntings use pre-laying climatic cues *per se* to time reproduction either at the population or individual level, the better the match between arthropod abundance and peak offspring demand, the higher the breeding mean productivity is for the population. Although the timing of reproduction appears to be a consequence of climatic circumstances, some individuals appear to match the timing of breeding and arthropod abundance better than others resulting in higher productivity. Whether certain individual female buntings are consistently better able to time their reproductive decisions remains to be seen. This type of analysis will only be possible with the collection of data from multiple breeding attempts within an individual across years thereby enabling a reaction-norm type of analyses to examine individual flexibility in laying decisions in response to inter-annual climatic variation (i.e., reaction norm Brommer *et al.* 2005). Lastly, to further test the match/mismatch hypothesis in reference to an optimal period of food availability, we calculated the difference between an individual female's realized amount of arthropods during her offspring provisioning period and either the maximum (or peak) 9-day window of arthropod abundance, or the 9-day abundance surrounding the midpoint of emergence (50% quartile date) of the total seasonal arthropod biomass. We found that individual snow buntings were able to fledge more chicks the closer their period of chick-provisioning was to the period of maximum arthropod abundance for the year. Furthermore, total biomass of the season factored into this relationship as individuals in years of higher relative total abundance not only fledged more offspring than those of lower abundance but fledged approximately the same number of offspring when mismatched than perfectly-timed individuals in lower abundance years. In contrast, we found no significant effect of mistiming on number of fledglings when we examined the period surrounding the midpoint of arthropod emergence. This suggests that arthropod availability in the Arctic is not a constant progression to a peak followed by a decline, but instead is highly variable, oftentimes lacking a defined peak.

Overall, these findings are particularly important for shedding light on the mechanisms by which climate change impacts the breeding decisions of Arctic fauna, as the literature is comparatively more mechanistically sparse concerning polar systems in general (Parmesan and Yohe 2003). Taken together, chapter two and three reveal that



while we have made significant progress in examining these linkages, there remains enormous complexities in determining the downstream impacts of both intra- and inter-annual variation in Arctic climatic conditions to predict the schedules of both arthropods and the species which depend on them for successful reproduction. Nonetheless, knowledge gained from this thesis can aid future researchers by suggesting new and improved techniques for modeling approaches, data collection and the interpretation of results.

## **LIMITATIONS IN DATA COLLECTION**

### **Climate-based Predictive Models**

We tested the accuracy of climate-based predictive models to evaluate their uses in forecasting or hind-casting arthropod availability in the low Canadian Arctic. We attributed much of the variation surrounding the predictive capability of these models to variation in climate, but also to inconsistency across variables in their model contribution, suggesting an influence of other unknown variables. A major potential contributor that should be included in future models is community dynamics and how these have changed over the course of modeled years (McMahon *et al.* 2011). For instance, on our study island, there has been a major decline in the Common eider (*Somateria mollissima*) colony since 2005 as a result of Avian Cholera (Descamps *et al.* 2012). Such a drastic reduction in nutrient input into the system has likely influenced resultant arthropod abundance across years. As such, including this ecological variable into future models may improve predictive capacity. Another avenue that may be used to improve models is the collection of environmental variables at emergence sites, i.e. on our island arthropod emerge from ponds thus measures of water depth, ice cover, and water temperature may be included as variables. Finally, since this arthropod system is generally closed from immigration of most arthropods being located on a small island that is separated from the mainland by a large bay, it may be useful to incorporate measures of previous-year arthropod abundance into the model as surviving adults in year 1 are required to produce decedents in year + 1.

## **Improving Arthropod and Snow Bunting Sampling**

A current limitation of our study pertains to the arthropod sampling protocol. First and foremost, even though we have access to on-site, daily variation in climatic variables, the arthropod samples were collected every other day. This approach creates a coarser resolution in the data, reduces the accuracy of the perceived arthropod availability throughout the season and limits the potential accuracy of modeling approaches. We tackled this constraint by dividing sampled days by 2 and extrapolated the values across both the un-sampled and sampled day as a proxy of daily abundance values. In the future, to obtain a more accurate measure of arthropod availability, samples should be collected every day and at a consistent time each day. Lastly, the sampling period (beginning and end, and the total seasonal duration of sampling) varied across years. We controlled for this variance by setting a uniform start and end time for our abundance measures. However, to obtain an accurate measure of arthropod availability during the Arctic summer across years, ideally sampling should always commence before emergence occurs and this period should remain consistent inter-annually. Furthermore, early sampling of arthropods could be used to examine the impact of early resource availability on reproductive decisions of the buntings such as lay date and clutch size. A final limitation to our study is the variability in reproductive data for snow buntings. Specifically, the amount and type of reproductive data for individuals varied across sample years, i.e., a number of individuals did not have all measures recorded (lay date, hatch date, clutch size, and number of fledglings) creating a discrepancy in the amount of data for each measure. Ideally, all reproductive measures should be taken for all sampled individuals to capture as complete and detailed picture of the breeding patterns exhibited by individuals in the population as possible.

## **Individual Variation**

Chapter three shed light on the degree of individual variation exhibited among snow buntings breeding at East Bay Island. While the large number of individuals allowed us to examine links and relationships between climate, resource availability, and reproductive measures, we were unable to test and explain much of the individual

variation. To better explain individual differences in breeding productivity outside of the influence of climate and resources, information on individual differences in provisioning capacity and food delivery rates to nestlings could be measured. By accounting for individual variation in resource gathering we would be able to determine its effect on reproductive output and overall breeding success. To further explain variation in models, the age of individuals (particularly the female) could be included to account for differences in reproductive investment and foraging ability (Forslund and Part 1995, Kunz and Orrell 2004, Ardia and Clotfelter 2007). In addition, the mass/quality of the fledglings may be included in the future in order to determine further fitness consequences of mistiming across individuals (McKinnon *et al.* 2012).

## **Climatic Data**

Climatic measures used for analyses in chapter two were collected at the study site (East bay/Mitivik Island) from an automated weather station. However, climate data is only collected for a limited time on the Island (June 1<sup>st</sup> – August 1<sup>st</sup>) based on the presence of researchers at the site. Ideally, climate sampling should be conducted earlier (April and May) in order to determine conditions at the study site prior to arthropod emergence and snow bunting arrival and breeding, however due to logistical and economic constraints, this is not feasible. In lieu of this, we determined pre-breeding temperatures in late May using data collected from Coral Harbour weather station (approximately 50km away). As this data is collected at a different location it may not be an accurate representation of fine-scale measures at the study site (such as wind speed and snow cover) but it is a reliable indication of larger-scale measures such as temperature.

## **Repeated Breeding Data**

Unfortunately, in our 7-year dataset, although we have 78 unique individual females, we only encountered 4 instances of inter-annual female recaptures. Thus, due to this extremely low rate of individual return to this breeding site, we lack the ability to test repeatability (*sensu* Lessells and Boag 1987) in reproductive timing (lay date, hatch date), investment (clutch size), and success (number of fledglings) for individuals breeding on

the island. Examining within-individual flexibility in reproductive phenology and success across years would allow us to determine whether individuals are capable of altering their breeding schedule and investment across years. Ultimately, these data would provide the opportunity to examine how changing environmental conditions are influencing individual reproductive decisions and therefore whether certain individual female buntings are consistently able to optimally time their reproductive decisions to maximize fitness remains to be seen (i.e., reaction-norm analyses Brommer *et al.* 2005).

## **CONCLUSION**

In summary, this thesis sought to examine how linkages between climatic variation in the Arctic, arthropod emergence and avian phenology influence fitness outcomes in snow buntings. We have examined the capacity for different types of climate-based models to predict arthropod abundance and emergence in the Arctic and speculated how they may be improved in the future. Results suggest that climate is differentially impacting arthropod and avian phenology. To this end, we examined the impact of resource availability on the reproductive success of buntings using a biologically-relevant window of resource demand in the buntings and determined that optimal matching resource abundance to demand maximizes the reproductive output of individuals. Lastly, we provide multiple avenues for future research to test underlying questions still unanswered and to further our understanding in this complex system, particularly in the context of climate change.

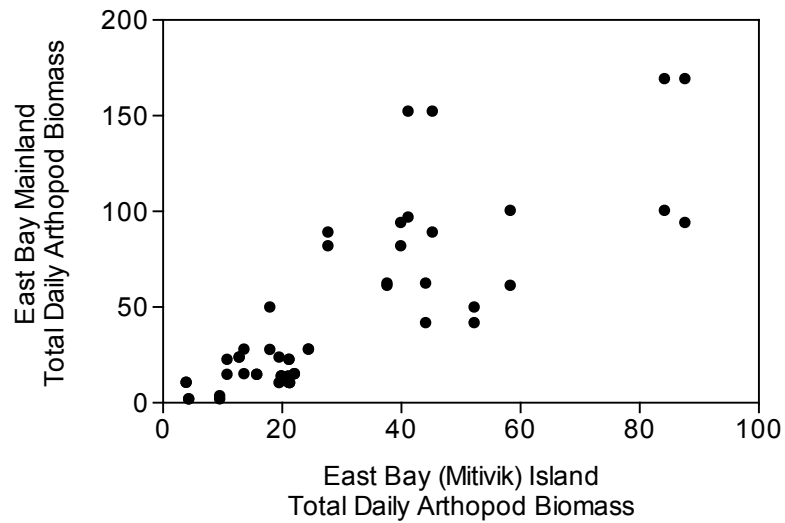
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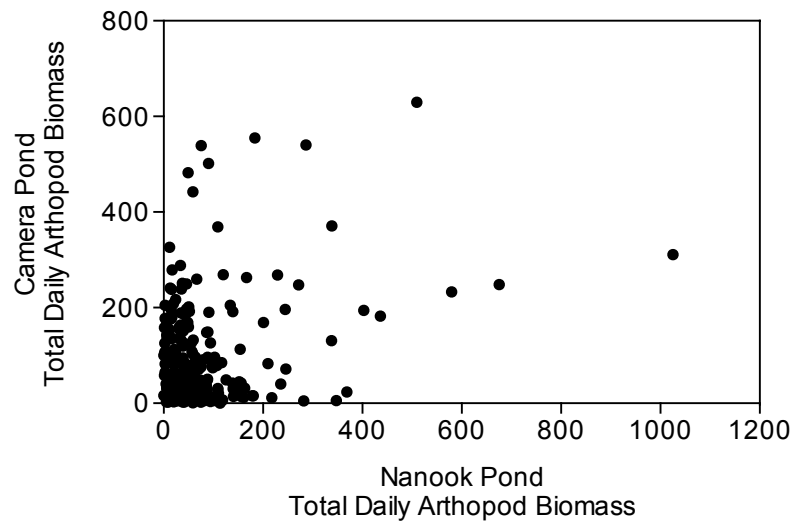
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## APPENDICES

Appendix A – Correlation of arthropod availability from 2013 and 2014 between East Bay mainland site and East Bay (Mitivik) Island site (Pearson pairwise correlation= 0.80,  $n= 49$ ,  $p= <0.0001$ ).



Appendix B – Correlation of arthropod abundance from 2009-2013 between arthropod sample trap sites (Camera and Nanook ponds) (Pearson pairwise correlation= 0.28,  $n=225$ ,  $p= <0.0001$ ).





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